SOCIAL INFORMATION GATHERING IN LEMURS

April M. Ruiz

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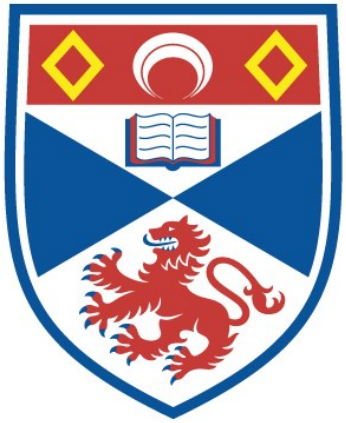

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by

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Abstract

By investigating the cognitive capacities of non-human primates, we can begin to understand the cognitive capacities of the evolutionary ancestors we share with these species. While there is a great deal of research exploring the socio-cognitive abilities of simian primates, prosimians have not been sufficiently studied. Without data from these species, our knowledge about the evolution of the primate mind is limited to the common ancestor shared between simian primates only, precluding understanding of the phylogenetic origins of certain phenomena.

I explored the socio-cognitive capacities of lemurs, a type of prosimian primate. I studied several areas of social cognition related to social referencing, defined as the ability to use and seek out social information when appraising objects or events. As social referencing is a popular subject in both human developmental and non-human primate literature, I aimed to determine how prosimians' capacities compare.

My research was conducted with captive lemurs of three species: *Eulemur fulvus fulvus*, *Eulemur macaco macaco*, and *Eulemur fulvus rufus*. I found that lemurs use social cues regarding food palatability to modify their own feeding behaviour and that they visually attend to conspecifics differently when presented with novel, as compared to familiar, foods. Lemurs also visually referred to a human experimenter's face when presented with an anomalous interaction and went on to engage in gaze alternation. Lemurs failed to use information about the experimenter's attentional state, however, when modifying their use of a trained gesture. Finally, I found that lemurs are able to visually co-orient with conspecifics, correctly prioritising

information from the head over that from the body, and that they go on to use conspecific gaze to locate hidden resources.

These results show that lemurs are more cognitively advanced than previously thought and the origins of some social referencing skills may be phylogenetically older than previously hypothesised.

Acknowledgements

I must begin by thanking Dick Byrne and Juan Carlos Gómez, my supervisors. For your unwavering support in scientific and personal matters, for being light-hearted and willing to play along with my rambunctious American attitude, and for having confidence in me when I was unable to do so for myself – I am extremely (and probably eternally) grateful.

Thank you to Jean-Jacques Roeder for allowing me to collaborate with him, always believing I could speak French better than I actually could, and for singing Frank Sinatra songs in the hallways of CdP. Fly me to the moon.

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Chapter 1

To live in a group is to live with competitors. Animals that rest, travel, forage, and play together are also in constant competition with one another for access to resources such as food and mates (Humphrey, 1976; Janson & van Schaik, 1988). However, group living can provide benefits that make it all worthwhile. The more individuals there are in a given area, the more likely it is that a predator will be detected and effectively escaped or defeated (Jolly, 1966; van Schaik, 1983; Strier, 2003). Although an individual might experience competition for access to food from group members, a group as a whole is better at monopolising a rich food source than an individual would be on its own (Wrangham, 1980; Wrangham, 1982; Janson & van Schaik, 1988; Strier, 2003). Being in a group that includes kin provides an individual with valuable allies (Chapais, 2001). And living in a group with others gives an individual the potential to obtain and use social information from them: this is the focus of my dissertation.

As animals go about their daily activities, their natural behaviour, including affective displays, object manipulation, and the directing of visual attention toward objects of interest (Coussi-Korbel & Fragaszy, 1995), potentially provides useful information to those around them (Galef & Giraldeau, 2001). One of the most interesting benefits of group living is the opportunity to gather information from other individuals by visually attending to them and then using that information in appraising objects or events, a mechanism called social referencing. The process of social referencing includes both the passive use of information that happens to be available

through the behaviour of others and also the active seeking of that information when it is needed (Feinman, 1982). Both methods enable an individual to learn important aspects of an object or event (e.g., its location, whether it is safe or dangerous) without requiring direct experience (Feinman, 1982; Klinnert et al., 1983; Phillips et al., 1992; Heyes, 1993).

By attending to group members' behaviour toward, or in reaction to, certain objects or events, an individual can learn a great deal (Range et al., In press). For example, seeing a conspecific spit out a piece of food could alert an observer not to ingest the same item. Or, following the direction of another individual's attention could facilitate an observer's detection of a predator or food resource. Individuals engaging in social referencing might be expected to alternate their gaze between a potential informant and an object of interest and should go on to modify their behaviour based on the information that was gained (Klinnert et al., 1983; Heyes, 1993).

Because individual learning can be a costly endeavour, as the rate of error can be high and errors can result in tragic outcomes, mechanisms like social referencing, which allow an individual to learn about objects in the environment without the need for direct experience, should be favoured through natural selection (Heyes, 1993; Boyd & Richerson, 1996). Given the highly adaptive value of social referencing abilities and the cognitive similarities between humans and other primates, it is possible that this mechanism is widely used in the primate order (Boccia & Campos, 1987). However, while many studies have focused on these abilities in simian primates (see chapters 3-5 for reviews), prosimian species have been neglected in comparative research efforts. Not only does this create a "taxonomic gap" in our understanding of primate cognition (Tomasello & Call, 1997), but it does so at a key

section of the primate evolutionary tree. Without data from prosimian primates, our knowledge about the evolution of the primate mind is limited to the common ancestor shared between simian primates only. To help fill this gap, my dissertation focuses on the social referencing abilities of a type of prosimian primate: the lemur.

In this introductory chapter, I will first provide some information about what lemurs are, and also review some of the work that has been done by other researchers exploring lemurs' cognitive capacities. To close the chapter, I will discuss the aims of my thesis and provide an overview of how I have organised the remaining chapters.

1.1 – Lemurs

Marty the Zebra: [about King Julian, a ring-tailed lemur] *He's got style.*

Alex the Lion: What is he, like, king of the guinea pigs?

Melman the Giraffe: I think it's a squirrel.

King Julian: Welcome... Please feel free to bask in my glow.

Alex the Lion: Definitely a squirrel.

Melman the Giraffe: Yep, a squirrel.

– Madagascar, a Dreamworks Animation film

Look! It's a pile of poo!

- Boy, 6, upon seeing a sleeping red-fronted lemur at Edinburgh Zoo

The name 'lemur' comes from the Latin word "lemures," meaning "ghosts" or "spirits" (not "poo"), and is a reference to many lemurs' nocturnal lifestyle, their

large, reflective eyes, and some species' eerie howling and screeching vocalisations. Unlike their squirrel look-a-likes, lemurs actually belong to a group of primates called the prosimians, from which the more highly derived simian lineage split off around sixty million years ago (Tattersall, 1982; Sauther et al., 1999; Yoder & Yang, 2004; Figure 1.1). Lemurs are found on the African island nation of Madagascar and a few

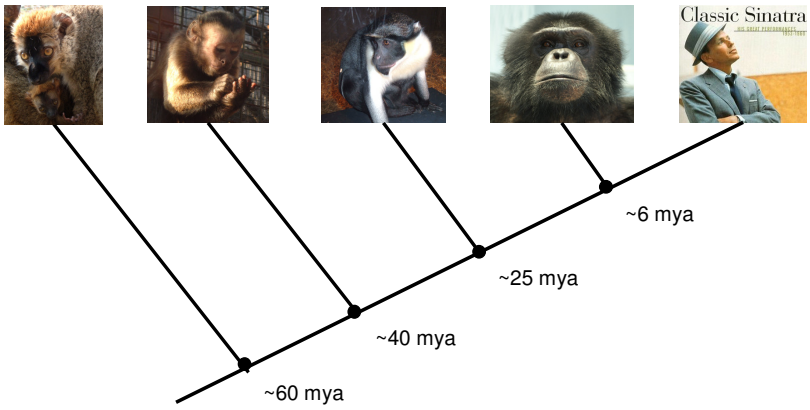

Figure 1.1 – A basic representation of the primate lineage. Primates to the left are most distantly related to humans, and primates to the right are more closely related. From left to right: prosimians (red-fronted lemur), New World monkeys (brown capuchin), Old World monkeys (Diana monkey), non-human great apes (chimpanzee, photograph by Marietta Dindo), and humans (Frank Sinatra, photograph from www.amazon.com). Listed are the dates, in million years ago (mya), of the last common ancestor shared with humans.

surrounding islands, such as Mayotte. Today, lemurs make up 13% of all living primate species (Martin, 2000), a relatively large proportion given the small size of Madagascar compared to the regions of Africa, Asia, and Central and South America where the rest of the primates are found. Lemurs are also one of the most threatened

primate taxa, partially due to the loss of between 80 percent and 90 percent of forest habitat on Madagascar, which has led to forest fragmentation limiting home ranges and genetic diversity (Lehman et al., 2006; Olivieri et al., 2008).

Lemurs are relatively small-brained (Armstrong, 1985) and are the most primitive group-living primate (Bearder, 1987; Richard, 1987), which means they are more like the original primates of tens of millions of years ago than are simian primates (Tomasello & Call, 1997). For example, lemurs have retained many ancestral mammalian traits, such as the possession of a wet rhinarium on the end of the nose, which aids in olfaction (Byrne, 1995; Sauther et al., 1999; Yoder & Yang, 2004). Nevertheless, like many simian primates, lemurs form complex groups composed of individuals of all ages and sexes, characterized by kinship and other relationships maintained through social play and grooming (Jolly, 1966; Richard, 1987; Pereira et al., 1990; Kappeler & Ganzhorn, 1993). As such, lemurs face social problems similar to those faced by group-living simians, such as learning the rank and behavioural patterns of other group members and engaging in social interactions accordingly (Jolly, 1966). Allison Jolly (1966) has written, "In social behaviour, as in anatomy, … lemurs are generally primate in structure." Research exploring the cognitive capacities of lemurs, however, is minimal and focuses mainly on non-social aspects of cognition, such as lemurs' ability to manipulate objects and their understanding of number and ordinal relationships.

1.1.1 – Early work

Harlow and colleagues (Harlow et al., 1932; Maslow & Harlow, 1932) conducted a series of studies exploring various primate species' performance on a

delayed response test. In this type of task, the experimenter allows the subject to witness the hiding of a food item in one of two locations. He then lets the subject search for the food after a set amount of time has passed, with the goal of determining how long the subject can wait before its ability to choose the correct hiding spot deteriorates. When comparing data across primate genera, researchers found that lemurs' search accuracy decreased sooner than that of monkeys and apes. These findings were corroborated by research conducted by Jolly (1964b).

Differences between lemurs and simian species were also found in the way in which individuals manipulate objects. Jolly noted that lemurs in the wild rarely manipulated inedible objects (1966) but did interact with items that were not baited with food in captivity (Jolly, 1964a; 1964b). However, researchers have reported that lemurs manipulated inedible objects in less diverse ways than simian primates did (Parker, 1973; Parker, 1974; Torigoe, 1985), as lemurs regularly picked up these items and transported them but failed to bring these items in contact with other objects through actions such as sliding, rolling, or throwing.

Davis and Leary (1968) tested both monkeys and lemurs in a bent-wire detour task, which requires a subject to move a piece of food to the end of a wire on which the food is threaded. This wire contains a series of L-shaped bends and, as such, subjects sometimes need to push the food away from them in order to succeed. Davis and Leary found that both Old and New World monkeys performed better on this task than lemurs did. Jolly (1964a, b) has also reported poor performance on puzzle tasks that require subjects to push an apparatus away from themselves or manipulate objects that are not in direct contact with a food reward in order to retrieve it.

Given lemurs' inferior performance on these types of tasks, as compared to that of simian species, Alison Jolly (1966) has concluded, "Lemurs show that primate society could develop without the particular cleverness of our own ancestors."

1.1.2 – Lemurs revisited

These early studies comparing lemurs' behaviour to that of simian primates helped to create an idea that lemurs' cognitive abilities are fewer and less varied than those of monkeys and apes. However, more recent work is challenging this impression, as researchers are now reporting performances on some tasks that are similar to those of simians.

Object manipulation

In response to early findings that lemurs manipulate objects in less diverse ways than simian primates do, Tomasello and Call (1997) cautioned that, as the objects were not presented with any potential goal, these studies only investigated subjects' ability to manipulate objects in the context of exploring objects for exploration's sake. They speculated that perhaps given motivation lemurs would be more interested in exploring and using items in more varied ways, which would show that a failure to display manipulation in a play context does not imply a lack of the capacity to understand object-object relations altogether.

Recently, Santos and colleagues (2005b) provided the context Tomasello and Call had called for by exploring whether lemurs recognise the functionally relevant aspects of tools. They reported that lemurs were able to manipulate tools to a more

useful position when these tools were oriented incorrectly. Further, lemurs correctly prioritised tool size, and appropriately ignored colour and texture, when choosing between two possible pulling tools with which to retrieve a food reward.

Numbers and ordinal relationships

Lemurs have also recently been shown to have relatively sophisticated numerical cognition abilities. In a paradigm traditionally used to explore what human infants know about number (Wynn, 1992), subjects are shown one object on a stage. The stage is then covered with a screen, behind which an experimenter places a second item. The screen is then lifted to reveal the expected outcome of two objects, or an unexpected event of one object, three objects, or one very large object. By measuring subjects' looking time, researchers have found that human infants can discriminate between the expected and unexpected events, suggesting a capacity for enumerating small sets of objects. In two studies with lemurs, researchers have shown that prosimians share this ability with humans (Santos et al., 2005a; Mahajan et al., In press).

To explore lemurs' understanding of ordinal relationships, MacLean and colleagues (2008) used a touch screen to present pairs of stimuli to lemurs in order to determine whether these animals are capable of transitive inference (i.e., given that A is greater than B and B is greater than C, the ability to reason that A is greater than C). In the first phase of the experiment, subjects were required to touch the higher ranking (as determined by the researcher) of two photographs and were trained on specific pairings (e.g., A and B, B and C). In the test phase, new combinations were presented (e.g., A and C). The researchers found that lemurs correctly chose the higher ranking

of the two stimuli in these novel pairings, suggesting that lemurs have transitive inference abilities.

Communication

Captive ring-tailed lemurs use different calls for different types of predators and respond differently to these calls in playbacks (Macedonia, 1990; Macedonia & Yount, 1991). Researchers reported that while lemurs first emitted a "gulp" in response to any predator, they followed by emitting different calls for aerial or ground predators. In playback experiments in which these calls were played through loudspeakers in the absence of a predator, researchers found that lemurs responded differentially to each type of call by using an appropriate escape strategy.

Another lemur species, the ruffed lemur, was not found to have similar referential signalling capacities (Macedonia, 1990).

Self-control

Genty and colleagues (2004) explored lemurs' capacity for self-control. In this type of study, subjects are presented with two arrays of food rewards, one consisting of more food items than the other. The subject is then allowed to reach for one in order to receive a reward. However, after the subject reaches for one array, the experimenter gives the subject the array it did not choose. As a result, subjects must suppress their tendency to reach for the larger reward and, instead, reach for the less desirable of the two options in order to receive the most food. In this task, lemurs were able to exhibit self-control by inhibiting their natural impulse to reach for the

larger of two rewards after training similar, both in number of trials and method, to training procedures used with simian primates (Silberberg & Fujita, 1996; Anderson et al., 2000).

1.1.3 – What about social cognition?

In 1997, Tomasello and Call pointed out that we know very little about prosimians in the domain of social cognition. Unfortunately, not much has changed in the last decade. But with growing evidence that lemurs share with simian primates many non-social cognitive abilities that researchers had expected they would not, it is possible that they also share many socio-cognitive abilities with simians, as well. Shepherd and Platt (2008) have reported that when lemurs are not moving around their environment (thereby, physical features of their surroundings do not require as much attention), they show a preference for visually attending to social stimuli, such as conspecifics and human experimenters. With special attention paid to other individuals, it is possible that lemurs gather and use social information in ways similar to other primates. However, research focusing on topics related to prosimian social referencing is lacking at best, leaving us with many unanswered questions about their cognitive abilities.

1.2 – General Aims

Povinelli and Eddy (1996b) put it simply: "We will never fully understand the true function of our own psychological structures until after we fully understand the

timing and purpose of their origin." I could not agree more. While comparative research with apes and monkeys is critical for understanding the evolutionary origins of the modern primate mind, prosimians are more like the original primates of tens of millions of years ago than are the simians (Tomasello & Call, 1997). As such, the earliest primate about which we can obtain insight through comparative research is the evolutionary ancestor common between lemurs and humans (Byrne, 1995). This opportunity should not be overlooked, as we will never gain a thorough understanding of the primate mind if prosimian species continue to be neglected in socio-cognitive research.

The aim of my dissertation work was to begin to explore several areas of social cognition that have been popular topics of research for those working with monkeys and apes, all of which have implications for the understanding of social referencing. As such, this dissertation includes three data chapters (chapters 3-5), each focusing on one of these topics. Within each data chapter I provide some background information about the topic, the details of two experiments concerning that chapter's topic, and a discussion of the findings. In chapter 2, I introduce the subjects that participated in these experiments and go over common experimental methods and procedures. In chapter 3, I discuss the gathering and use of information from social sources in a foraging context. In the first experiment, I provided lemurs with palatable or unpalatable food items and examined the feeding behaviour of those individuals who had witnessed their group member consume or reject food. In the second, I went on to explore whether lemurs exhibit differential looking strategies when presented with novel, as compared to familiar, foods in order to investigate whether they actively seek out information from others. In chapter 4, I examine social referencing during social interactions and also whether lemurs modify their behaviour depending

on the human social cues with which they are presented. In the two experiments detailed in this chapter, I presented lemurs with an anomalous social situation and measured whether they used gaze alternation as a visual monitoring method and whether lemurs adjusted their behavioural responses according to my attentional state. In chapter 5, I explore gaze following and whether lemurs use the direction of another individual's gaze to locate hidden objects. In the first experiment of this chapter, I explored whether lemurs follow the gaze of conspecifics and what cues they use when doing so. In the second, I presented lemurs with conspecific gaze cues in a modified object-choice task in order to explore whether gaze following has any consequence for subsequent action. Finally, in chapter 6, I discuss the results of all six experiments together in order to put lemurs into the larger picture of primate social cognition and briefly discuss whether lemurs are capable of mental state attribution.

Through these experiments and discussions, I hope to provide useful insight into the evolution of primate cognition and to open opportunities for further work, which I hope that researchers, including myself, will be able to take on in the near future.

Chapter 2

In this chapter I will provide information about the subjects that participated in my experiments, as well as testing procedures that were common to all experiments I conducted as part of my PhD work. I will also explain how experimental trials were recorded and coded for the analyses described in chapters 3-5.

2.1 – Subjects

The lemurs that participated in these experiments came from two sites: the Centre de Primatologie de l'Université Louis Pasteur in Strasbourg, France, and the Blackpool Zoo in Blackpool, England, United Kingdom.

2.1.1 – Centre de Primatologie

At the Centre de Primatologie, subjects were four adult brown lemurs (*Eulemur fulvus fulvus*, Figure 2.1): Hyacinthe (Hy), a female, and her offspring Hutch (Hu), a male, and his sisters Honorine (Ho) and Hermine (He); and three adult black lemurs (*Eulemur macaco macaco*, Figure 2.2): Rousse (Ro), a female, her sister Rustine (Ru), and Philémon (Ph), an unrelated male.

All subjects were born at the centre and each species was socially housed in an enclosure consisting of both an outdoor (8.0 X 2.9 X 2.6 m) and indoor (4.9 X 2.1 X

Figure 2.1 – Brown lemur (*Eulemur fulvus fulvus*), subjects Hutch (Hu; left) and Hermine (He; right)

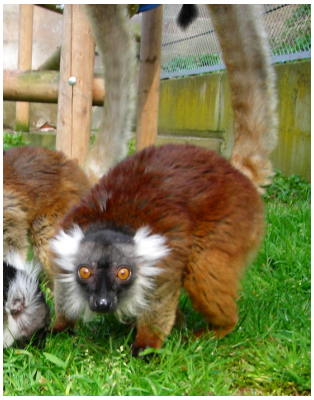

Figure 2.2 – Black lemur (*Eulemur macaco macaco*), subject Rousse (Ro)

2.6 m) compartment furnished with tree trunks and shelters. A tunnel between these two sections could be closed in order to isolate subjects for testing. All lemurs had been trained to enter the inside compartment individually and had previously participated in several cognitive studies in this manner. In addition, the tunnel in the black lemur enclosure could be further divided into two separate chambers, and animals were trained to enter these areas individually as well. Except during test

sessions, lemurs were able to move freely between the outdoor and indoor areas and tunnels.

During the course of my research, the brown lemur group also included an adult male named Haribo, who preferred not to participate in experiments and, sadly, died in early 2007. Also present was a juvenile female, Hevea (daughter of Hyacinthe), who was not yet comfortable interacting with experimenters on her own. The black lemur group also consisted of an adult female, Rebecca (mother to Rousse and Rustine), who also died in early 2007. Rousse gave birth to two females, Roxanne and Ratatouille, in the spring of 2007.

The lemurs were provided with commercial primate pellets each day, and with fresh fruit and vegetables once a week. Water was available *ad libitum*, and lemurs were neither food- nor water-deprived for testing

Of particular interest is this group of lemurs' previous training to indicate choices of stimuli by using an abbreviated reaching gesture, or 'point' (Genty et al., 2004; Genty et al., 2008; Genty, personal communication). During training, the experimenter sat in front of the lemurs' enclosure and presented the subject with a pivoting platform, in the middle of which was a pile of raisins, a preferred food. The subject was permitted to reach through the wire mesh of its enclosure to retrieve the raisins. After a few sessions, the experimenter moved the platform a bit further away from the enclosure. When the lemur extended its arm through the mesh to attempt to grab the raisins at this new distance, the lemur was unable to reach. After the subject extended its arm through the mesh, however, the experimenter rewarded its attempt by moving the platform closer to the enclosure so the subject could retrieve the reward. As the training went on, the experimenter moved the platform farther and farther away from the enclosure so that

Figure 2.3 – Pointing in lemurs. A still video image of Hutch (Hu) using a trained pointing gesture.

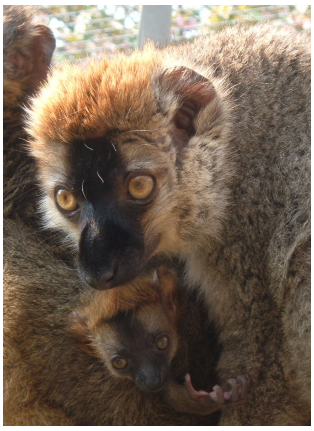

Figure 2.4 – Red-fronted lemur (*Eulemur fulvus rufus*), subject Jack (Jk)

lemurs could not even come close to reaching the raisins. The experimenter continued to reward subjects for extending their arm through the wire mesh, a behaviour that would have been futile otherwise. Genty (personal communication) reported that lemurs abbreviated their reaching over time by no longer fully extending their arms

nor positioning their hands in an attempt at grasping. Further, lemurs went on to use this abbreviated reach to select choices of stimuli in a variety of contexts, generalising the behaviour to a number of tests. An example of lemurs' pointing is provided in Figure 2.3.

2.1.2 – Blackpool Zoo

At the Blackpool Zoo, subjects were three adult red-fronted lemurs (*Eulemur fulvus rufus*, Figure 2.4): Roxanne (Rx), a female; Scortcha (Sc), a female; and Jack (Jk), a male. Lemurs inhabited an enclosure consisting of an indoor (3.3 X 2.6 X 2 m) and outdoor (14.7 X 4.5 X 3.0 m) compartment, and were able to move freely between them at all times.

Unfortunately, these animals were not trained to participate in cognitive studies and it was not possible to separate individuals for testing. Instead, I presented stimuli to subjects from the side of their home enclosure and discarded trials in which there were distractions from other individuals or zoo visitors (see chapter 4 for further information).

This group of lemurs consisted of one more adult female, Gwendolyn, who did not participate in my experiment, and who gave birth to an infant in the experiment's final weeks.

The lemurs received a mixture of fruits, vegetables, seeds, and commercial primate chow twice a day. Water was available *ad libitum*, and animals were neither food- nor water-deprived for testing.

Information regarding the experiments in which subjects participated can be found in Table 2.1.

Table 2.1 – Subject participation. This table lists all subjects that contributed to my dissertation, and indicates in which specific experiments subjects participated.

Subject	**Chapter 3**		**Chapter 4**		**Chapter 5**	
Name (Abbr.)	*Exp 1*	*Exp 2*	*Exp 1*	*Exp 2*	*Exp 1*	*Exp 2*
Hyacinthe (Hy)			X	X	X	X
Hutch (Hu)			X	X	X	X
Honorine (Ho)			X	X		X
Hermine (He)			X	X	X	X
Rousse (Ro)	X	X	X	X		X
Rustine (Ru)	X	X	X	X		X
Philémon (Ph)	X	X				
Jack (Jk)					X	
Scortcha (Sc)					X	
Roxanne (Rx)					X	

2.2 – Video recording and coding

Each trial of every experiment was recorded using a Sony DCR-HC19E miniDV camcorder situated behind the experimenter. I uploaded these videos to a PC and analysed them at 0.08-second intervals using Microsoft Windows Movie Maker

version 2.1. During recording, I provided the date, subject name, and trial numbers in order to correctly match video with paper records detailing conditions run and any other important notes. As the video camera was always situated behind me, photographic stimuli were seen on video from the back only (chapter 5), and my attentional cues were not visible (chapter 4). As such, blind coding was possible.

Chapter 3

Some plants use toxic substances, such as alkaloids, to defend themselves from potential consumers (Glander, 1982). While the concentration of alkaloids decreases as fruit ripens, making these items more palatable and safe to eat, not all plants provide clues to palatability through appearance (Prescott et al., 2005). There is great risk in individual sampling when noxious substances might be present and, given this potential cost, there should be a selective advantage for individuals able to use social cues to assess food quality (Fairbanks, 1975).

The experiments detailed in this chapter explore whether lemurs seek out and use social cues while feeding. In Experiment 1 I examined whether lemurs are able to modify their own behaviour toward food after having witnessed a conspecific reject food of the same kind. In Experiment 2 I presented lemurs with novel and familiar food items to determine whether they seek out social cues when presented with foods with which they have had no prior experience.

3.1 – Experiment 1: Do lemurs automatically use information available from conspecifics?

Benefiting from social foraging depends on successfully reading information-bearing cues given by other group members, yet many of these cues do not seem to have been shaped by natural selection for a communicative purpose (Markl, 1985).

One example is a typical disgust expression, which an individual emits in reaction to sampling distasteful food. This reaction typically involves spitting out the distasteful food item and sticking out one's tongue and, as this behaviour is found even in decerebrate rats, is considered to be a reflexive behaviour (Grill & Berridge, 1985; Snowdon & Boe, 2003). As a consequence, an animal producing a natural reaction also happens to provide potentially useful information to anyone observing it. Social referencing is one way social animals can take advantage of this information and involves two "defining components," as described by Russell and colleagues (1997). Firstly, the individual seeking information must look at the individual providing the information, as well as at the object or event that needs to be evaluated. Secondly, emotional information must be gathered to determine whether the referent is positive or negative and, thereby, how to react to it.

Evidence that primates are able to use information provided by conspecifics regarding food palatability is mixed. Cotton-top tamarins were shown to socially learn an aversion to tuna, a preferred food, when it was made unpalatable by treating it with white pepper (Snowdon & Boe, 2003). In baseline trials, before adulterated tuna was introduced, all individuals regularly sampled tuna. In test trials in which tuna was adulterated, however, only a few members of each test group sampled the tuna. Those that did sample the tuna exhibited typical disgust reactions and also decreased the number of food calls they emitted. As pilot work revealed that monkeys could not gather information about the palatability of the adulterated tuna through olfaction or sight, it follows that members of the group that never sampled the adulterated tuna gathered some information from those that tasted the tuna first, and used this information to modify their own behaviour. It is unclear, however, whether tamarins

were responding to the visual disgust reaction of conspecifics, a decrease in food calls, their group members' subsequent avoidance of the food, or some combination.

Hikami (1991) explored whether witnessing a conspecific avoid a specific food has any effect on an observer's feeding decisions. Japanese macaque mothers were made to be averse to their infants' preferred food by a cyclophosphamide (a chemical that induces gastrointestinal illness) injection administered after consumption. As a result, these adults would avoid this food when presented with it. In the test phase, infants were allowed to feed with their mothers, and presented with a choice between their preferred food and another food. Two out of three infants tested decreased their preference of the previously preferred food after witnessing their mothers avoid it. These results, Hikami asserted, provided evidence that Japanese macaques are able to gather socially valuable information about food palatability. Hikami and colleagues (1990) provided further evidence that Japanese macaque infants are influenced by their mother's food preferences in another study. Here they tested Japanese macaque mother-infant pairs to see whether social information could extinguish a conditioned food aversion. Infants were conditioned to be averse to two foods by a cyclophosphamide injection, and each infant's mother was conditioned to be averse to only one of these foods. After the aversions were established, mothers and infants were put together in the same enclosure and presented with both foods. The mothers avoided only the food to which they were averse and readily consumed the food to which they were not averse, as was expected. After being exposed to their mothers' behaviour, infants began to eat the food to which their mothers were not averse, despite having been averse to it themselves. Infants did maintain their aversion for the food to which their mothers were also averse, and therefore avoided. In other words, a conditioned aversion was

extinguished through witnessing the behaviour of a conspecific. The authors claimed that the results of these two studies were evidence of social transmission of food preferences.

In a similar paradigm, while behavioural cues available from conspecifics helped unrelated common marmoset subjects to overcome a food aversion, a conditioned food aversion was not socially transmitted to naïve individuals (Queyras et al., 2000). To begin, the researchers determined that all subjects highly preferred food A to food B. The researchers then conditioned an aversion to preferred food A in some individuals by treating the food with a high concentration of salt. After this treatment, conditioned individuals showed a preference for food B and avoided food A. Next, conditioned and unconditioned individuals were allowed to feed together, and were presented with both foods, which were both now untreated. After the unconditioned monkeys reached for food A, the conditioned subjects began to eat it as well, reverting to their original food preference. When later presented with both foods in the absence of the unconditioned individuals, the conditioned subjects continued to eat food A. Months later, Queryas and her team conducted a control test to determine whether the extinction of subjects' aversion occurred over time without social input, or if the social information provided by the unconditioned conspecifics was necessary. They reconditioned their subjects to be averse to food A, and re-presented them with a choice between foods A and B. They found that subjects did not return to preferring food A over time without social input, indicating that marmosets were able to gather social information about food palatability and use it to modify their own behaviour. However, it is worth noting that the unconditioned individuals did not use conditioned subjects' avoidance of food A to modify their behaviour. It seems that information

about what foods were palatable was socially transferred, but not information about what foods were unpalatable.

Free-ranging spider monkeys were also shown not to use social information to avoid foods that group members found to be distasteful (Fairbanks, 1975). Bread was dyed to mark it as unpalatable and then treated with one of four agents: quinine, hot pepper, salt, or ipecac emetic. The experimenter then placed these items, in addition to bread that was undyed and untreated, at a popular feeding site. Subjects showed clear signs of disgust, including vomiting, after sampling the marked food, and did not try the food again after one or two direct experiences. However, all subjects tried all foods available at least once, not taking into account the experiences of their conspecifics, and thereby showed no signs of observationally learning that the marked food was not safe to eat.

In a study with captive mandrills, Jouventin and colleagues (1977) provided adult individuals with two types of banana. One type was cut into slices and then dyed red using a tasteless food colouring, and so remained palatable. A second type was cut into slices, dyed blue, and then treated with quinine to make the banana bitter. They allowed infant mandrills to witness the adults feed, without allowing the infants access to the food themselves. The adult mandrills avoided the blue banana and ate the red. Next, infants were given a tray containing both blue and red banana. Infant subjects successful avoided the blue slices, showing they learned something about the relative palatability of the two foods. But in a similar study with chacma baboons and vervet monkeys, Cambefort (1981) found that baboon observers preferred to taste the palatable food first, but also went on to taste the unpalatable food, providing them with direct experience on which to rely when making discriminations later, while vervet observers tasted both items indiscriminately. Unlike the mandrills, then,

chacma baboons and vervet monkeys seemed unable to use social information regarding food palatability. But unlike the experiment with mandrills, Cambefort's study was conducted in a free-ranging context.

Boinski & Fragaszy (1989) also reported a case in which free-ranging primates were unable to use social information when making foraging choices. They found that while wild infant squirrel monkeys sometimes avoided noxious prey with which they had previously witnessed other infants having difficulty, these instances were few. The researchers reported that infants mainly fed in the company of other inexperienced infants, rather than seeking out information from experienced adults, and that most of what infants learned about which foods were appropriate to eat was done so individually.

To be sure potential observers have witnessed pertinent social information in a natural context is near impossible given the distance between individuals and the presence of visual barriers (e.g. foliage) and distractions (Fairbanks, 1975). As a result, one cannot be certain whether a lack of learning is due to an inability to learn or merely a missed opportunity to see a conspecific accept or reject a food item. Jolly (1966) has contended that captive experimental set-ups are one way to effectively direct a subject's attention to a desired object or action, allowing researchers to better explore cognitive abilities.

Additionally, it has been suggested that social learning can only occur when a behaviour is performed, not when there is a lack of behaviour (Visalberghi & Fragaszy, 1996). Perhaps, then, noticing food *avoidance* is not sufficient to elicit a strong, reliable response in observers, but witnessing a *rejection* of food at close range would be (Visalberghi, 1994). Combined, these two factors – whether the observers actually observe, and the presence or absence of something to observe – might explain

some of the differences in experimental results. Perhaps Boinski and Fragaszy's (1989) infant squirrel monkeys were too distracted by the environment to take much notice of their group member's reactions with any reliability. Or maybe the demonstrator's avoidance of food in Cambefort's (1981) vervet monkeys was just not as salient as a disgust reaction, such as that found in Snowdon and Boe's (2003) cotton-top tamarins, would have been.

Given these possible contributing factors to the disparate results reported above, I aimed to design an experiment in which subjects had clear opportunity to witness social information, and in which the cues subjects would observe would be more salient than mere food avoidance. In the experiment that follows, I investigated whether lemurs were able to use social information about food palatability to modify their own behaviour toward familiar food items. To ensure subjects witnessed a conspecific's reaction to unpalatable food, I tested individuals in pairs, indoors, and away from their social group. This arrangement both reduced distractions and brought each subject into close proximity to a feeding conspecific. I provided one individual of the pair (the Model) a portion of palatable or unpalatable food and allowed it to sample the food. Next, I presented the second individual (the Subject) with its own portion of food. In order to assess whether lemurs are able to use information provided by others, I measured subjects' behaviour toward their own portion of food after they witnessed a conspecific accept food and also after they witnessed a conspecific reject food.

3.1.1 – Method

Subjects

Subjects were three black lemurs at the Centre de Primatologie: Philémon, Rousse, and Rustine, as described in Chapter 2.

Testing chambers and apparatus

The testing area consisted of two adjacent chambers separated by a sliding wire-mesh door. This set-up allowed a lemur in one chamber visual, auditory, and limited tactile access to an individual in the next chamber (Figure 3.1).

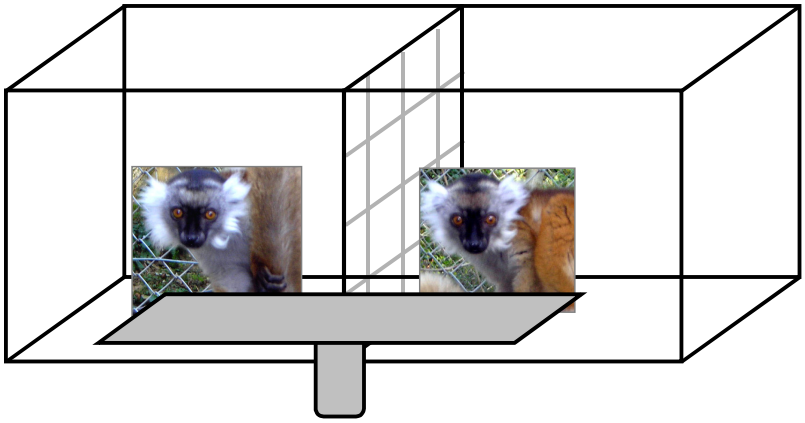

Figure 3.1 – Experimental set-up. Subjects sat in adjacent testing chambers, separated by a wire mesh door. A platform was placed in front of the chambers so that half its length was in front of each chamber.

These chambers were situated on top of a short concrete wall (approximately one meter in height) that extended past the front of the chambers, creating a 20cm-wide shelf along the front of the chambers. A platform (60 X 18 X 25cm) was placed

here, flush against the front of the chambers. The front panels were also wire-mesh, which allowed lemurs to reach through and manipulate objects presented on the platform.

Procedure

For each trial, one lemur was seated in each of the two testing chambers, with the wire mesh door closed between them. The presentation platform was situated so that half of its length was in front of either side. I was seated in the front and centre of the two chambers and, as they were at a height of approximately one meter, I was able to remain out of the immediate view of the subjects.

To begin each trial, I raised my hand, which held ten pieces of a familiar food, above the centre of the platform in order to attract individuals to the apparatus if they were not already seated there. I then placed the food in front of one individual (Model) and, after 15 sec had passed, I then reached up and placed ten pieces of food in front of the second individual (Subject). A trial ended 60 seconds after the Subject received its portion of food, at which point I removed any remaining food items.

Four familiar foods (apple, peach, grape, and melon) were used in two types of trials: Baseline and Test trials (Table 3.1). In Baseline trials, both the Model and Subject received ten pieces each of the same unaltered food (e.g. unaltered apple). In Test trials, the Model received ten pieces of an altered familiar food (e.g. altered apple). Altered foods were soaked in tonic water for 24 hours to make them unpalatable, yet non-toxic and unchanged in visual appearance.

To be sure that lemurs found the altered food to be unpalatable, I presented altered fruit to another group of black lemurs also at the Centre de Primatologie. This

group was composed of four adults (two males and two females) and, though highly habituated to human experimenters, were not trained to participate individually in cognitive experiments. I entered their home area, scattered the altered fruit on the ground, and allowed them to sample it. Upon tasting altered food items, lemurs stuck out their tongues, removed the food from their mouths, and then allowed the food to drop onto the ground. I felt these were clear signals that the lemurs found the altered food to be distasteful, and proceeded to prepare the food in this way for testing.

As I was interested in determining whether the Model's behaviour alone would change the Subject's behaviour, I divided Test trials into two groups: True and False. In the True test trials, the Subject received ten pieces of the same altered food

Table 3.1 – Trial types. Unaltered familiar foods were palatable, and altered familiar foods were soaked in tonic water to make them unpalatable, but indistinguishable by sight.

Trial type	*Model receives…*	*Subject receives…*
Baseline	Unaltered	Unaltered
True	Altered	Altered
False	Altered	Unaltered

the Model had received 15 seconds earlier (e.g. altered apple). In this case, the Subject received true information about the food's palatability. In order to be sure that the Subject's behaviour was not affected by some cues inherent in the food itself, I also conducted False test trials in which the Subject received ten pieces of the same type of food (e.g. apple) the Model had received, but the unaltered version instead. In this case, the Subject received false information about the food's palatability.

The experiment was designed so that each individual served both as Model and Subject in each possible dyad for each food in all conditions. Baseline trials of each type (e.g. Baseline trial using grape) were given to each Model-Subject combination once, resulting in each individual serving as Subject for a total of sixteen Baseline trials. To avoid habituation, each individual served as the Subject only once for each food in each of the two Test conditions (e.g. Rousse was Subject only once in a True test trial using apple). As such, each individual completed eight trials in each of the two Test conditions. Each dyad was given two trials each day so that each individual in a given pair was able to act as Model and Subject. As a result, each lemur participated in four trials per day: two as the Subject, and two as the Model.

Analysis

For each trial I recorded the Subject's latency to food handling (defined as the time between the presentation of food and the first time the subject grasped the food). I predicted that if lemurs are able to use social information, then they should alter their behaviour accordingly in response to that information. Specifically, Subjects should exhibit increased latency to handling food in the Test condition.

I also measured the Subject's looking time, defined as the total time spent visually attending to the Model's behaviour in the first 15 seconds of each trial, which was the period before the Subject received its own potion of food. This measure would determine whether lemurs found the behaviour of a conspecific that was feeding to be more salient than the behaviour of a conspecific that rejected food, or vice versa. Significantly different average looking times could affect subjects' latency. If lemurs were distracted by the Model's behaviour, their distraction, rather

than the information gathered by having observed the Model, might affect their latency to handling food.

One True test trial for Philémon was removed from analysis due to external distractions, and one False test trial for Rustine was removed from analysis due to a video error.

In order to assess inter-observer reliability, an experimenter not associated with the study coded 20% of trials. Pearson's correlations revealed a high level of agreement for both looking time (r=0.76, P<0.001) and latency to food handling (r=0.96, P<0.001).

3.1.2 – Results

Looking time

I measured each Subject's looking time to explore whether Subjects spent more time looking at the Model in Baseline versus Test (True and False, combined) conditions to determine whether either the Model's food acceptance or rejection was more salient to the observer. If so, lemurs might have been visually focused on the Model unequally between conditions. If lemurs were distracted by the Model's behaviour in such a way, their distraction, rather than the information gathered, might affect their latency to handling food. I found no support for this possibility, as no Subject's average looking time per trial was significantly different between conditions (Ph: independent $t(29)$=1.12, P=0.90; Ro: independent $t(29)$=0.78, P=0.44; Ru: independent $t(29)$=1.20; P=0.24; Figure 3.2).

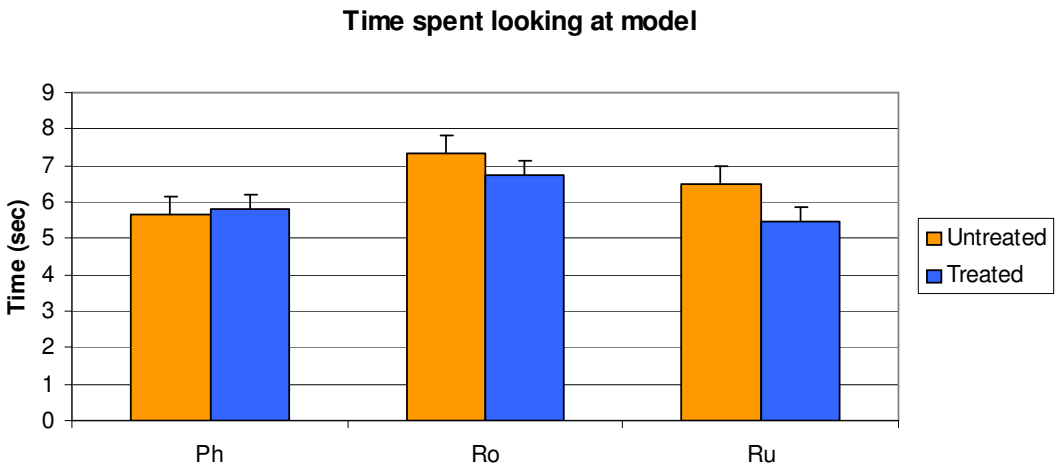

Figure 3.2 – Average time spent looking at the Model. Before the Subject was presented with its own portion of food, the average amount of time it spent looking at the Model. Data is divided into trials in which the Model had untreated (palatable) or treated (unpalatable) food. Whiskers represent standard error of the mean. No significant differences were found.

Latency to handling

Given the skewed nature of the data, I conducted non-parametric statistics (exact Mann-Whitney U) to compare each individual's latency to handling the food between conditions.

I first compared latency to handling palatable and unpalatable food for each individual when serving as the Model (Figure 3.3). As a Model, a lemur had not seen any relevant social cues and, as such, it should not have exhibited any difference in its latency to handling palatable or unpalatable food unless it were responding to olfactory cues signalling the food had been altered. I found no significant differences (Ph: U=97.0, z=1.20, *P*=0.25; Ro: U=72.5, z=1.71, *P*=0.10; Ru: U=105.5, z=0.28,

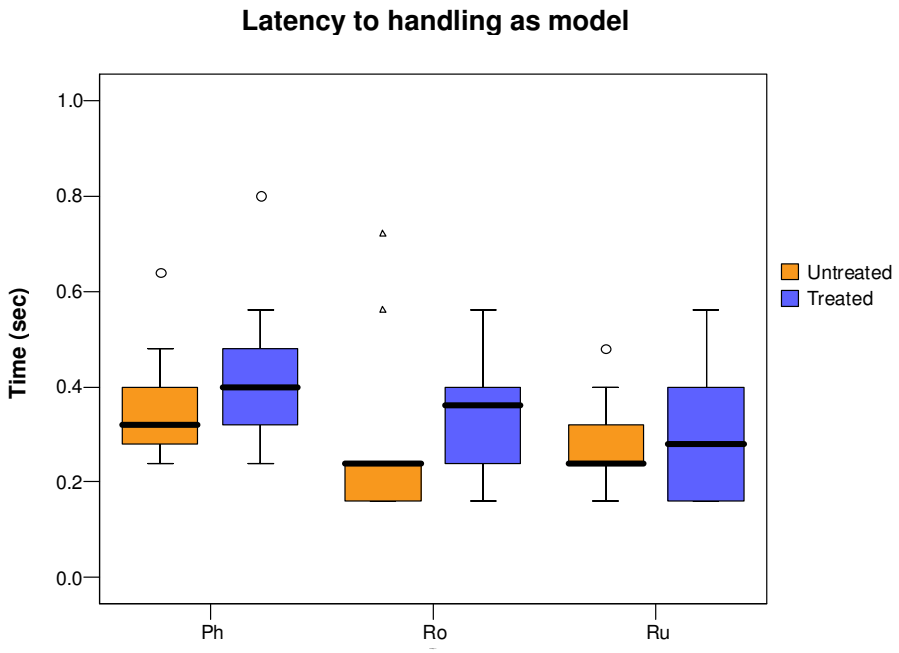

Figure 3.3 – Latency to handling as model. For each individual, when serving as the Model, the time between the presentation of food and the act of handling food when that food was untreated (palatable) or treated (unpalatable). As the Model, the subject has no social information about food palatability. Bold lines represent the median latency, the boundaries of each box represent the inter-quartile range. Whiskers represent the range, while outliers are marked by circles and triangles. No significant differences were found.

P=0.79), indicating that lemurs could not tell the difference between the unaltered and altered food until they were able to bring it to their face for sniffing or tasting.

To determine whether subjects behaved differently after seeing a conspecific accept or reject food, I compared each Subject's latency to handling food in the Baseline and Test trials. All three subjects appear to exhibit increased latency in the Test condition (Figure 3.4), with a significant effect found for two out of three

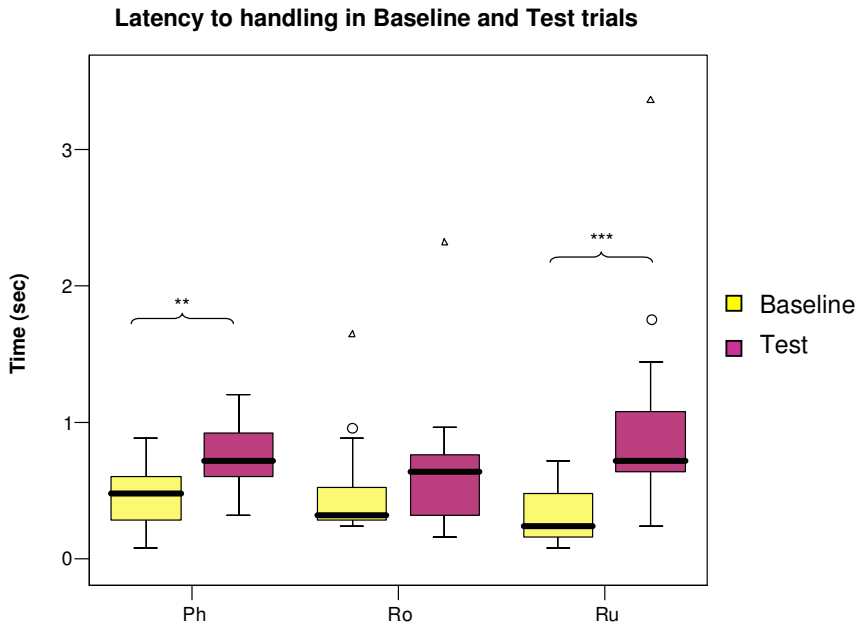

Figure 3.4 – Latency to handling in Baseline and Test trials. For each subject, the time between the presentation of its portion of food and handling of the food in Baseline and Test trials. Bold lines represent the median latency, the boundaries of each box represent the inter-quartile range. Whiskers represent the range, while outliers are marked by circles and triangles.

Mann-Whitney U test: ** $P<0.01$, *** $P<0.001$

subjects (Ph: U=45.0, z=2.81, $P=0.004$; Ro: U=91.5, z=1.14, $P=0.264$; Ru: U=29.0, Z=3.63, $P<0.001$).

To confirm that lemurs' behaviour was not a result of cues provided by the food itself, I also compared Subjects' latency to handling food in the True and False test conditions. If lemurs could detect the quality of the food without gathering social information, then they should exhibit a decreased latency in False trials – in this case the Subject saw the Model reject unpalatable food, but went on to receive palatable

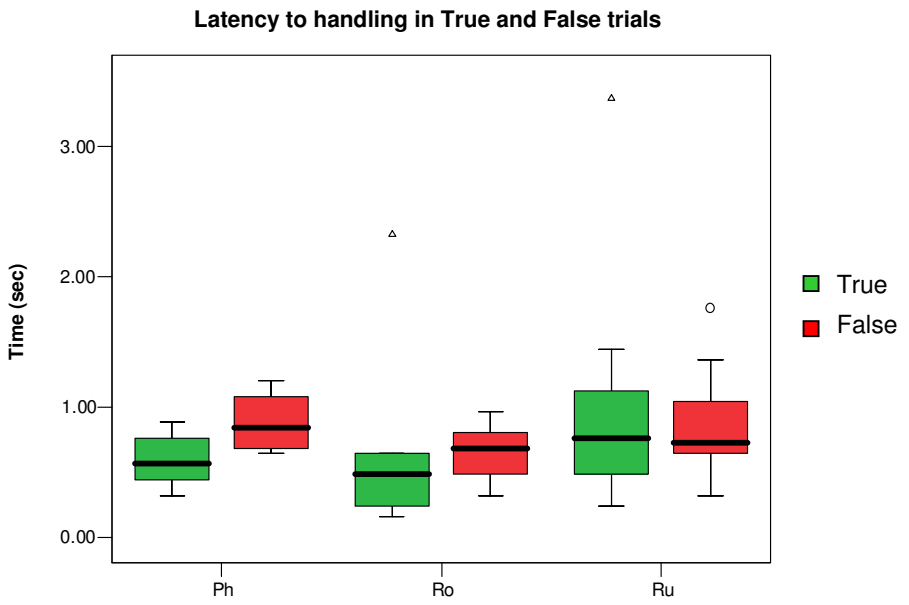

Figure 3.5 – Latency to handling in True and False test trials. For each subject, the time between presentation of its own portion of food and handling of that food in both True and False test trials. Bold lines represent the median latency, the boundaries of each box represent the inter-quartile range. Whiskers represent the range, while outliers are marked by circles and triangles. No significant differences were found.

food for itself. This was not the case, as no subject's latency was significantly lower in the False condition (Ph: U=11.0, z=1.98, *P*=0.054; Ro: U=19.0, z=1.40, *P*=0.20; Ru: U=25.0, z=0.35, *P*=0.78; Figure 3.5).

It is possible that lemurs exhibited decreased latency to handling food in Test trials simply as a result of response facilitation (Clayton 1978, Byrne 1994), rather than having gained information about food quality. As response facilitation increases the frequency of certain behaviour in one individual in the presence of others engaged in that behaviour, perhaps lemurs are not as motivated to eat when a nearby

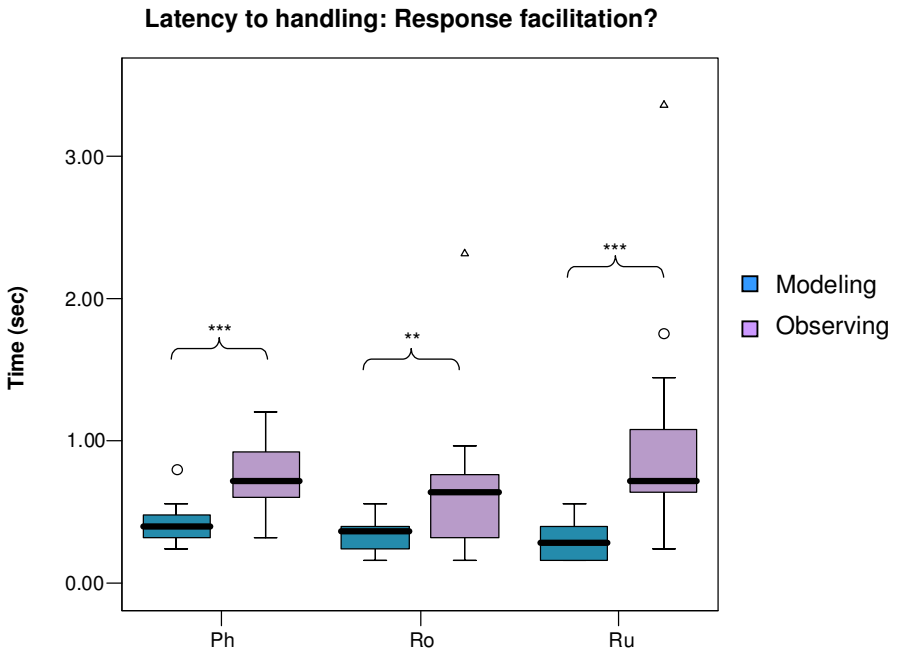

Figure 3.6 – Latency to handling: Response facilitation? For each individual, the time between the presentation of its own portion of food and handling that food. The "modeling" data represent trials in which the individual acted as the Model, and was thereby in the presence of a conspecific that was not eating, as that individual had not yet received its own food. The "observing" data represent trials in which the individual acted as the Subject, and was thereby in the presence of a conspecific that was not eating because that individual had rejected its food. Bold lines represent the median latency, the boundaries of each box represent the inter-quartile range. Whiskers represent the range, while outliers are marked by circles and triangles. Mann-Whitney U test: ** P=0.01, *** P<0.001

conspecific is not eating. To test this, I compared lemurs' latency to handling when they received unpalatable food as a Model to when they, as Subjects, had just witnessed a Model receive unpalatable food. In the former case, a conspecific – the Subject – was present and not eating as it had not yet received its portion of food. In the latter case, a conspecific was also present and not eating, but the individual had witnessed that conspecific's initial rejection of food. If lemurs' decreased latency in

Test trials as compared to Baseline trials is due to the mere presence of a conspecific that is not eating, then there should be no difference in latency to handling food between these two circumstances. I found that this was not the case, as lemurs exhibited significantly higher latency to handling when provided with social information about food palatability (Ph: U=30.0, z=3.58, $P<0.001$; Ro: U=52.0, z=2.51, $P=0.01$; Ru: U=25.5, z=3.76, $P<0.001$; Figure 3.6).

Although lemurs were slower to handle food after having seen a conspecific reject a food item of the same kind, all subjects did bring the food to their faces in all trials. After doing so, lemurs tossed the food aside without inserting it into their mouths if it was treated, or consumed it if it was untreated. As lemurs would frequently cover their muzzles with their hands in this process, sniffing and licking behaviour could not be reliably and systematically measured for cross-condition analyses.

3.1.3 - Discussion

Despite spending the same amount of time looking at a conspecific no matter what it was doing, two out of three lemurs' feeding behaviour was influenced by what they saw. Subjects took longer to take food items presented to them after having seen a group member's disgust reaction to, and later rejection of, that same food. However, subjects were not completely persuaded to avoid the food after seeing these reactions.

In this study, I treated food with tonic water to make it distasteful for the Test condition. It is possible that this alteration was not enough to elicit a strong avoidance reaction in my Subjects, as the cost of trying the food was very low. Unlike studies using chemicals that induce gastro-intestinal illness, the greatest risk lemurs endured

in my experiment was an unpleasant taste, and it might be that lemurs would have modified their behaviour more clearly if the cost of error were higher.

Further, as I used foods with which subjects were familiar, the lemurs I studied had had years of experience of these foods being palatable. In a study with Japanese macaques (Matsuzawa & Hasegawa, 1983), researchers found that subjects became averse to novel foods treated with cyclophosphamide more quickly than they did to familiar foods treated with the same chemical. Later in the study, when extinction of the aversion was explored, subjects quickly resumed eating the familiar food while continuing to avoid the novel food. And in Fairbanks' study with free-ranging spider monkeys (1975), all subjects had previous experience with marked bread being safe, as they had been presented with dyed, but untreated, bread in pilot sessions. Perhaps, then, the monkeys' previous experience hindered their ability to respond properly to group member's disgust reactions in test sessions. These results suggest that a familiar food that has been made to be merely distasteful, as in my experiment, would be slow to elicit an avoidance response in subjects who have witnessed a group member experience these foods.

It is also possible that, since food was presented to subjects by a familiar human experimenter, lemurs were more inclined to sample the food. Japanese macaques are known to eagerly accept novel foods from people visiting the park in which they live (Wantabe, 1989), and free-ranging rhesus macaques were found to be more likely to sample novel foods given to them by human experimenters than novel foods encountered on their own (Johnson, 2000). In both cases, monkeys had extensive history of humans providing safe and palatable food, which seems to have developed into an expectation of the same. Perhaps this phenomenon is also at work in the current study.

The salience of the model's reaction might also play a role. Infant chimpanzees withdrew from a novel object more often when having received a fear message from a human caregiver (Russell et al., 1997), and monkeys developed a fear of snakes after observing a conspecific's fear reaction toward a snake (Mineka et al., 1984). In these cases, the social information provided was very effective in eliciting differential behavioural responses in subjects. Urgent vocal signals, body posture, facial expressions, and possibly frantic movements convey information in many domains, whereas the behaviour associated with refusing to eat distasteful food is less arousing and exists mainly in the visual domain alone. It has been suggested that visual cues on their own are not sufficient to result in social learning about food (Visalberghi & Addessi, 2001).

Snowdon (2001) has argued that primates that are too sensitive to social cues risk missing out on a potentially valuable food resource. For example, while a particular food might be unpalatable at the time an observer witnesses a conspecific tasting, and then rejecting, it, that same food could be palatable later. If an observer is very sensitive to the information provided by its group member regarding that food's palatability, it might never again sample the food, thereby missing out when it is safe to eat. This would limit the diet of that individual, which can be a costly result. The ability to respond to environmental change (e.g. fruit ripening) is critical to many primate species (Prescott et al., 2005). Perhaps, then, the lemurs in my experiment were correct in sampling the food despite the reactions of their group members. It could be beneficial to be willing to taste items while having the predisposition to discard those items if there is the slightest problem. This predisposition could be established through witnessing social cues, such as a disgust reaction.

It remains to be determined whether the behavioural differences found in my study are the result of information about the specific food in a given trial having been gathered, or whether Subjects' behaviour is a result of the Model's behaviour alone. Research with capuchin monkeys (Visalberghi & Addessi, 2000) showed that subjects ingested more food when in the presence of feeding conspecifics, even if they were eating different foods. This could be a result of a mechanism such as response facilitation (Byrne, 1994), a social effect in which witnessing a conspecific perform a specific action increases the probability an observer will perform the same action. If this type of mechanism is at play in foraging contexts, Visalberghi and Addessi (2000) contend that the result would be a very unsafe way to integrate foods into one's diet. They argue that an observer could end up eating something nearby that is noxious because a conspecific in its view is eating a different food. King (1994) has pointed out, however, that foraging primates that are in close proximity to one another are likely to be feeding on the same food in natural conditions. Perhaps, then, a mechanism such as response facilitation is an adequate, although not perfect, one for a primate to use.

It is possible that a conspecific's rejection of food affects the attitudes of an observer that are not specific to that food, but equally result in appropriate behavioural responses. In other words, the negative reaction witnessed by an observer can possibly lead the observer to feel stress, affecting their behaviour generally. This behaviour change would not be specific to the food that the observer witnessed its group member eat, but it could lead the observer to avoid that food all the same. A similar possibility has been raised regarding emotional information provided by human mothers to their infants (Feinman, 1982). The non-specific effect of attitudes on behaviour (sometimes referred to as "emotional contagion," (Feinman, 1982)) can

effectively yield emotional responsiveness without an observer drawing conclusions about a specific referent. However, it has been shown that human children do use specific information when deciding whether to eat novel foods (Addessi et al., 2005). Perhaps human and non-human primates, then, cope with social information using different cognitive mechanisms.

By exploring latency to handling food, rather than using a gross measure such as whether or not subjects tasted food items, I found that visual cues do, in fact, affect an observer's behaviour. It may be the contribution of other factors, such as prior experience, the source of the food, and salience of a conspecific's cues that influence an observer to avoid a food completely rather than to proceed with caution.

In this experiment I showed that lemurs are able to respond to information provided by a conspecific in a way that is beneficial. This can only attest, however, to their observational learning ability. Observational learning occurs when one individual observes another's action and goes on to internalise what was observed (Bandura, 1986). This type of learning does not require conceptualising another individual as a carrier of information, as the learner simply profits from observing the relationship between another's physical actions and the consequences of those actions. Learning occurs without having consulted the other individual as part of a purposeful search for information, and even without recognising that information has been obtained (Baldwin & Moses, 1996). Active information seeking stands in contrast to observational learning, as an individual that is able to actively gather information avoids relying on chance observations. Instead, this individual is able to recognise situations in which information is required and is able to alter its own behaviour in order to obtain it. In the next experiment I explored whether lemurs are

good information seekers by determining whether they visually refer to other individuals differently when they need information, as compared to when they do not.

3.2 – Experiment 2: Do lemurs actively seek out information from conspecifics?

Food neophobia, the hesitancy to eat novel foods (Barnett, 1963), is an effective way to avoid consuming potentially dangerous substances. It is also important, however, for generalist primate species to exploit new resources (Visalberghi, 1994; Galef & Giraldeau, 2001). Taken together, these two approaches seem irreconcilable: individuals of any generalist species in a risky environment should investigate, taste, and eventually incorporate novel foods into their diet, but should also be very cautious as there is a risk of ingesting noxious substances (Rozin, 1977). As such, any behaviour that increases the probability of eating safe items should be favoured (Galef, 1993).

One way in which generalist primates might manage to reconcile neophobia and neophilia is by trying novel foods in a social context. It would be beneficial to forage with others when confronted with an unfamiliar food source, as group members can provide valuable information about palatability (see Experiment 1). The presence of group members, then, may help an individual to overcome neophobia and thereby result in that individual sampling more items. When feeding on familiar food, however, it should not be necessary to gather information. As such, the presence or absence of group members should not affect an individual's feeding patterns.

In a study with brown capuchins, subjects' consumption of familiar food was not found to vary based on the presence or absence of conspecifics, but subjects were more likely to try unfamiliar foods in the presence of others than when alone (Visalberghi & Fragaszy, 1995). In a similar study with common marmosets, Voelkl and colleagues (2006) explored the role of social contact on infants' reaction to novel foods. In a 2X2 design, they presented infants with familiar and novel foods in the presence or absence of group members. They found that while infants readily approached, tasted, and consumed familiar foods irrespective of the presence of conspecifics, their behaviour toward novel food was markedly different. When alone, infants exhibited higher rates of exploratory behaviours (e.g. sniffing), and often refused to eat the food. If infants did consume novel food in this condition, it was in small amounts only. Conversely, when allowed to feed with group members, infants consumed more novel food and exhibited fewer exploratory behaviours.

In another study with juvenile common marmosets, Vitale and Queyras (1997) found that subjects did not need to be feeding alongside conspecifics in order to overcome their neophobia. In their study, they reported that juveniles ate more novel food when merely allowed visual access to group members than when isolated from the group, but did not show the same difference in consumption when presented with familiar foods. Conversely, for human children the mere presence of others is not enough to help overcome food neophobia. Harper and Sanders (1975) found that children were more likely to eat new foods when an adult was also eating that food than when an adult just offered it to them.

Fragazsy and colleagues (1997) have suggested that when primates seek information from others about novel foods, they should do so through actively approaching, and interacting with, others that are eating those foods. While these

methods would indeed be useful, they may not be the only ways in which primates gather information. On Koshima Island in Japan, Wantabe (1989) reported that the consumption of fish spread through a group of Japanese macaques in a manner suggesting social transmission of the behaviour. He noted, however, that there was little evidence the transmission occurred through means of close social interaction, and did not propose an alternative explanation. This study highlights the lack of experimental evidence we have about exactly how social influences on food choices occur. If not through close contact with an individual who is eating food, then how?

Visually attending to others is one way in which primates can seek out and obtain information from conspecifics while not being in their immediate physical proximity. Some researchers have speculated that the ability to coordinate behaviour or benefit from another individual's experience can be achieved through social monitoring in addition to direct interaction (Cambefort, 1981; Coussi-Korbel & Fragaszy, 1995). Russell and colleagues (1997) agreed, and suggested that visual attention data should be collected in studies exploring the effect of social context on primates' behaviour toward novel foods.

Studies exploring visual attention have supported the idea that primates observe others when presented with unfamiliar items. Field observations indicated that infant mantled howler monkeys attended to their mothers' behaviour when encountering potentially novel leaves (Whitehead, 1986). Captive experiments revealed that young chimpanzee subjects looked to their mothers (Itakura, 1995) and human caregivers (Russell et al., 1997) more often when presented with novel toys.

In a study conducted by Addessi and colleagues (2007), Goeldi's monkey subjects were presented with novel foods while in a testing chamber adjacent to one in which group members were present. For each trial, group members were either

presented with food that was visually identical to the food the subject had, food that was visually different from the subject's food, or no food at all. Subjects visually attended to group members more often when group members were eating food that looked the same as the subject's own food than when group members were merely present and did not have any food. When group members were eating foods that were different than those the subject had, subjects did not visually attend to these individuals significantly more than when group members were present and without food. These results suggest that Goeldi's monkeys are capable of varying their visual attention to others depending on the situational context, attending more when conspecifics can potentially provide useful information, and less when they cannot.

Ueno and Matsuzawa (2005) found that infant chimpanzees paid more attention to their mothers when confronted with novel food items than familiar ones, and suggested that the congruence of novel items eventually consumed by both mothers and their infants in their study was largely the result of the infants' propensity to visually refer to their mothers. Social referencing, they argue, is a method infant chimpanzees might use to cope with neophobia and thereby expand their food repertoire.

The studies reviewed above show that simian primates might use social referencing as a way to cope with novel or otherwise ambiguous situations. By visually attending to other individuals, an observer can gather useful information when presented with unfamiliar items. But do prosimian primates also possess this skill? In the current experiment, I aimed to explore whether lemurs also seek out information from conspecifics using visual attention. The subjects were black lemurs, a species that has been shown to be food neophobic (Gosset & Roeder, 2001). I tested individuals in pairs, allowing only limited tactile contact with one another in order to

fully explore their use of visual attention during feeding. If lemurs seek out information from other individuals, they should exhibit a difference in visual attention toward conspecifics when presented with novel, as compared to familiar, food items.

3.2.1 – Method

Subjects

Subjects were the three black lemurs that participated in Experiment 1: Philémon, Rousse, and Rustine.

Testing chambers and apparatus

The testing chambers and apparatus were the same as those used in Experiment 1 (Figure 3.1).

Procedure

For each trial, one lemur was seated in each of the two testing chambers, with the wire mesh door closed between them. The presentation platform was situated so that half of its length was in front of either chamber. I was seated in the front and centre of the two chambers and, as they were at a height of approximately one meter, I was able to remain out of the immediate view of the subjects.

To begin each trial, I raised both my hands, each of which held ten pieces of the same food, above the centre of the platform to attract subjects to the apparatus. I

then moved my hands so that one was above either side of the platform and then simultaneously deposited the food items on each side. I then returned my hands to my lap, allowing subjects access to the food. I stopped each trial after 60 seconds and removed any remaining food.

Two conditions were tested:

Familiar – The food items used in the Familiar condition were ones the subjects received on a regular basis as part of their normal feeds. These were banana, carrot, and raisins.

Novel – The food items used in the Novel condition were ones the subjects had never before encountered. To determine with which foods lemurs were unfamiliar, I spoke with the veterinary staff, the caretakers, and research staff about what foods lemurs were given throughout the year and what foods had been given as rewards in other experiments. I then compiled a list of foods I wished to use in the Novel condition, and checked with the aforementioned individuals once again to be certain that the lemurs had never before tasted these foods. The Novel foods chosen and verified were mango, kiwi, red pepper, yellow pepper, fig cereal bar, biscuit, cantaloupe, red gel candy, dried apricot, pineapple, green pepper, bread, orange gel candy, courgette, avocado, litchi, walnut, potato, Sharon fruit, raspberry, cucumber, mushroom, strawberry, and pomegranate.

When possible, foods were cut into pieces measuring approximately 1cm X 1cm. Otherwise, foods were given whole (e.g. pomegranate seeds and raisins). Each novel food was used for one trial only to ensure familiarity was not established.

Trials were given so that each pair of subjects was given sessions of two trials, one Familiar and one Novel, each day. Overall, each subject completed sixteen Familiar trials and sixteen Novel trials.

Analysis

For each trial, I recorded how many times subjects looked at the model during the course of the trial and how much time subjects spent looking at the model.

One Novel food trial for the Ph-Ro dyad was removed from analysis due to a video error.

In order to assess inter-observer reliability, an experimenter not associated with the study coded 20% of trials. Pearson's correlations revealed a high level of agreement for total looking time (r=0.69, P=0.001), number of individual looks (r=0.73, P<0.001), and length of individual looks (r=0.82, P<0.001).

3.2.2 – Results

Looking time

To explore whether subjects paid more attention to their testing partner when presented with novel foods than they did when presented with familiar foods, I compared, for each subject, the average time spent looking at the test partner per trial in each the Novel and Familiar conditions (Figure 3.7). One out of three subjects spent significantly more time looking at its test partner in the Novel condition than in the Familiar condition (Ro: independent t(29)=2.85, P=0.008), while one subject

showed a trend in this direction (Ru: independent $t(30)=1.74$, $P=0.09$). The third subject did not show any significant difference between these conditions (Ph: independent $t(29)=0.34$, $P=0.74$).

Length of looks

In addition to total time spent looking at a test partner during each trial, I also explored whether there was a difference in the way in which subjects looked (Figure 3.8). For example, subjects could use a cursory monitoring strategy in which they make frequent, but brief, glances to their testing partner. Alternatively, subjects could make fewer looks toward their testing partner, but look for a longer period each time they do so. It has been argued that longer individual glances serve to allow an observer to extract more information about causal relationships, the consequences of actions, and other types of information that would be more difficult to gather by using a cursory monitoring strategy (Cohen, 1972; Range & Huber, 2007). Two out of three subjects employed the former strategy in the Novel condition, as compared to the Familiar condition. In other words, these individuals exhibited longer individual looks when confronted with novel food items than when given familiar food items (Ro: independent $t(175)=7.44$, $P<0.001$; Ru: independent $t(118)=2.70$, $P=0.008$). One subject did not show any significant difference in average length of individual looks (Ph: independent $t(81)=0.32$, $P=0.75$).

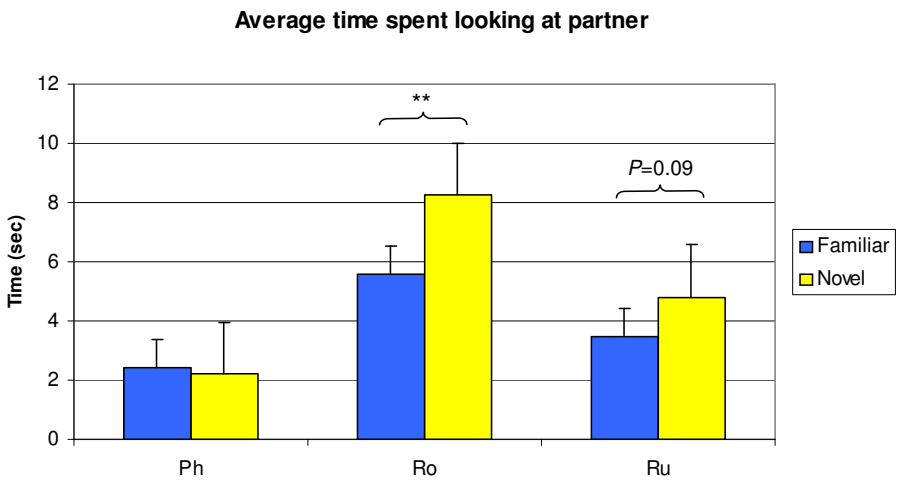

Figure 3.7 – Average time spent looking at testing partner. For each subject, the average time spent looking at its testing partner per trial in the Familiar and Novel conditions. Whiskers represent standard error of the mean. Independent *t*-test: ** $P<0.01$

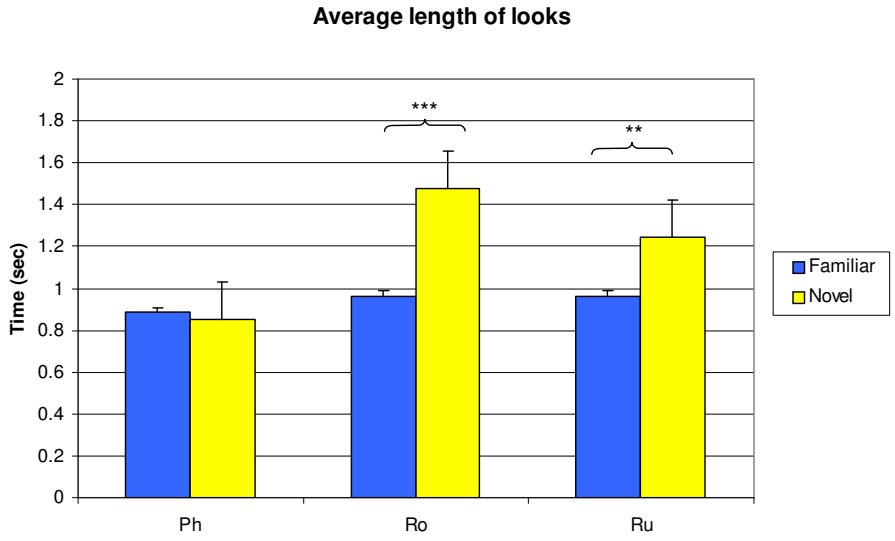

Figure 3.8 – Average length of looks. For each subject, the average length of each individual look made toward its testing partner in the Familiar and in the Novel conditions. Whiskers represent the standard error of the mean. Independent *t*-test: ** $P<0.01$, *** $P<0.001$

Individual differences

The subject who failed to exhibit any significant differences in behaviour between the two conditions in either of the above measures was Philémon. As such, I explored his looking behaviour further. Overall, Philémon looked at his test partner less often than the other two subjects, Rousse and Rustine, did. When comparing, between subjects, the percent of trials in which individuals looked to their test partner once only or not at all, I found that Philémon did so in significantly more trials than Rousse and Rustine did (26%, 3%, and 6% of trials, respectively; X^2=7.82, df=2, P=0.02).

3.2.3 – Discussion

In the above experiment, only one lemur spent significantly more time looking at a testing partner when presented with novel or familiar foods, and one more showed a trend in the same direction. However, Cohen (1972) has pointed out that total looking time might not be the whole story when exploring visual attention, as divergent attentional mechanisms can result in the same total looking time. One of these is a cursory monitory strategy in which an observer makes frequent, but brief glances, toward an object or event of interest. Alternatively, an observer can look fewer total times, but spend a longer amount of time looking with each glance. Two subjects in my experiment exhibited the latter strategy in the Novel condition, as compared to the Familiar condition. Both attended to a conspecific for longer each time they looked when presented with novel foods. As subjects had their own portion

of the same novel food, this behavioural difference suggests that subjects may not be interested in the food alone, but instead in the information a conspecific can provide about it. Using longer individual looks can allow observers to witness longer sequences of actions and thereby extract more information about the consequences of those actions, and other types of information that would be more difficult to gather by using a cursory monitoring strategy (Cohen, 1972, Range & Huber, 2007). Similar effects have been found in keas (Range et al., In press), common marmosets (Range & Huber, 2007), and human children (Range et al., In press).

One subject did not exhibit a change in looking behaviour between conditions: Philémon. Moreover, Philémon looked at his testing partner significantly fewer times overall when compared to the other two subjects. One possible explanation would be his status within the social group. Philémon is a male of a species that is characterized by agonistic female dominance (Fornasieri et al., 1993). As such, females supplant males at feeding sites (Fornasieri et al., 1993) and regularly initiate bouts of aggression, with little to no reconciliatory behaviour (Roeder et al., 2002). Males also do not compete with females for access to limited food resources (Roeder et al., 2002). Further, females have been shown to affect male black lemurs' performance in behavioural studies. In a task involving manipulating boxes in which food was hidden, males avoided proximity to female subjects and thereby remained at a distance from the experimental stimuli. As a result, males were never able to solve the manipulation task, either through a lack of opportunity to learn socially or a lack of contact with the box (Gosset & Roeder, 2000).

Coussi-Korbel and Fragaszy (1995) suggest that competing attentional demands in an individual's environment limit the amount of time that individual can spend looking at any one conspecific, event, or object. They argue that subordinate

squirrel monkeys, which live in large groups characterised by a hierarchical social organisation, would not be able to focus on any one individual for more than a few moments at a time due to frequent scanning of the environment, while high-ranking individuals would not have the same problem. Perhaps, then, Philémon's subordinate social status affected his looking.

As my study comprises only one male in my subject set, further study into this species needs to be done in order to determine whether Philémon's performance would be typical of male black lemurs. Further, similar looking time measures should be used to test species with divergent social systems to determine whether social status is indeed a factor in visual attention strategies.

3.3 – General Discussion

Drapier and colleagues (2003) have argued that information obtained by observing the feeding behaviour of others is much more than the acquisition of visual information alone, as the taste of scraps left behind from a feeding individual provides very useful information. Fragaszy and colleagues (1997) have also suggested that information gathering with regards to food should occur through interaction with individuals already eating that food. In both Experiments 1 and 2, I gave subjects limited access to their testing partner in order to study their use of visual information when unable to utilise the information gathering methods discussed by the researchers above. The results obtained by using this paradigm show that lemurs are sensitive to information gathered by seeing a conspecific's rejection of food (Experiment 1) and that lemurs also seek out information from conspecifics by employing different visual

attention strategies when presented with novel, as compared to familiar, foods (Experiment 2).

While sniffing the food items a group member is consuming and tasting its leftovers are undoubtedly effective ways in which to gain information about food palatability, only those closest to that individual would be able to access these items and obtain this type of information. And, even then, there would be limited availability of these items, leaving most group members without an opportunity for contact due to competition. For group-living primates, then, the capacity to use visual attention to actively seek out and observe a group member's behaviour, and then use the information obtained in modifying their own behaviour, can be key (Cambefort, 1981; Coussi-Korbel & Fragaszy, 1995; Russell et al., 1997). In this chapter I have shown that lemurs possess this capacity.

Chapter 4

In Experiment 2 of the previous chapter, I explored lemurs' use of social referencing in a foraging situation involving novel food. In that study, lemurs employed differential looking strategies depending on the uncertainty of the situation: they directed longer individual glances toward a testing partner when presented with food with which they had no prior experience than when they were presented with familiar food. In the two experiments that follow in this chapter, I aimed to determine whether lemurs also look to others for information in ambiguous social circumstances.

In Experiment 1, I investigated not only whether lemurs seek out social cues when presented with an ambiguous interaction, but also whether they use these social cues to modify their own actions, as measured through lemurs' use of gaze alternation and a trained pointing gesture. In Experiment 2, I again explored whether social cues affect lemurs' use of pointing in a paradigm more closely related to the conditions under which they were trained to use this behaviour. Before detailing the methods and results of these studies, I will begin by briefly reviewing literature that has explored this topic in non-human primates and human children. In this way I will arrive at the paradigms I ultimately chose as good ones to use with my lemur subjects.

Gaze alternation and its role in social interactions

Walden & Ogan (1988) suggest that an infant's looking at a parent's face could reveal that she understands the face as an important source of information. In their research group's studies, the direction of infants' looking was recorded after they

had been presented with novel toys. Infants aged between 6 and 40 months (Walden & Ogan, 1988; Walden & Baxter, 1989) all looked to their parents. However, an important difference in looking emerged: infants in the age groups of 13-23 months and 24-40 months looked to their parents' faces more often than those in the 6-12 month age group. These younger infants instead focused on any part of their parents' bodies. The authors suggested that the older infants were attempting to gain information about the objects by seeking out social cues from their parents, while the younger infants were instead establishing the continued presence of their parents because they felt uneasy about the situation. Dickstein & Parke (1988) explored infants' looking further and found that 11-month-old infants quickly alternated their gaze from an object of interest to a parent's face. They argued that the temporal link between the two looks indicated the infants sought information from the adult about the object specifically.

In a study with juvenile chimpanzees, Russell and colleagues (1997) examined whether subjects would alternate gaze between a novel object and a human caregiver, just as human infants do (Walden & Baxter, 1989; Dickstein & Parke, 1988). They found that all their chimpanzee subjects alternated gaze in a three-look sequence (object-caregiver-object) at least once, and 65% of subjects engaged in longer strings. These results suggest that chimpanzees, like human infants, engage in social referencing and use gaze alternation as a way to gather information about a novel object or event. This is not the only context, however, in which gaze alternation might occur.

Chimpanzees have also been found to alternate gaze between a desired object and the face of a human experimenter while using pointing or begging gestures (Tomasello et al., 1985; Leavens et al., 1996; Krause & Fouts, 1997; Leavens &

Hopkins, 1998; Leavens et al., 2004). Face-directed looks in the case of gestural communication might not serve as a way to evaluate an ambiguous situation, but instead a requester might look to another's face simply to check if they are paying attention to their gesture. As a result, the requester may alter his behaviour accordingly (Bruner, 1975; Tomasello, 1995). I will discuss this topic more thoroughly in the next section.

An additional, related, purpose of gaze alternation would be to establish mutual attention. Gómez (1991) has suggested that when one individual is requesting something of another, it is crucial for him to know if that other individual perceives his request. Attentional contact, Gómez argues, would be an indicator that the requester perceives that the helper perceives his gesture, resulting in effective communication and a fulfilled request.

The use of gaze alternation during the use of requestive gestures, such as pointing and begging, has been studied in a variety of non-human primates. In a study with squirrel monkeys (Anderson et al., 2007), subjects were required to point toward one of two cups in order for a human experimenter to give them a piece of food hidden underneath. While pointing, subjects alternated glances between the food and the experimenter's face quite rapidly. If the subjects were attempting to establish mutual attention, then they would have engaged in more gaze alternation or spent more time looking at the experimenter's face when the experimenter was looking back at them. Although they frequently checked the face of the experimenter, monkeys did not alter their looking behaviour in response to changes in the attentional state of the experimenter. Perhaps, then, squirrel monkeys did not look to the experimenter's face for mutual attention purposes. Instead, monkeys could have

referred to the experimenter's face in anticipation of a cue that they were about to receive food.

Another New World monkey, the capuchin, exhibited different behaviour in a similar study involving pointing. Hattori and colleagues (2007) reported that capuchins spent more time looking to an experimenter's face when that experimenter was looking back at the subject, as compared to when the experimenter was looking elsewhere. Unlike the study Anderson and colleagues conducted with squirrel monkeys, Hattori and collaborators did not observe any of their capuchin subjects engage in gaze alternation between a desired food object and the experimenter's face at any point in the study. The authors do admit, however, that these animals were observed to engage in gaze alternation spontaneously during normal feeds, and perhaps the artificial circumstances of the experiment (including the requirement to use a trained gesture) somehow affected their behaviour. Perhaps, then, it is best to explore gaze alternation under natural circumstances, rather than requiring subjects to use behaviours they have come to learn through extensive training.

In a study with children with and without autism, Phillips and colleagues (1992) predicted that children should look for social cues when an experimenter performed an anomalous action. In control trials, the experimenter presented subjects with a normal interaction in which he handed a toy to the child and allowed the child to take it. In test trials, however, the experimenter withdrew the toy just as the child reached for it, and kept it for 5 seconds before giving it to the child. The researchers scored whether the child looked to the experimenter's face after receiving the toy in control trials and after it was taken away in test trials. They found that typical children looked to the experimenter's face significantly more often in test trials than in control trials, and that children with autism not only failed to exhibit a difference in looking,

but also looked to the experimenter's face less frequently overall than typical children did. While typical children instantly alternated their gaze from the toy to the experimenter's face in test trials, children with autism remained focused on the toy itself, or sometimes looked to the experimenter's hands. The researchers claim that referring to the experimenter's face is an indication that the children without autism sought information about the experimenter's goal or intentions. If they were most interested in a mechanistic explanation for the toy's withdrawal, then they, too, should have focused on the toy or on the experimenter's hands.

This type of paradigm provides a simple way to explore face-directed looking in both verbal and non-verbal subjects, without needing to employ artificial factors such as a trained gesture. As such, Phillips and colleagues' paradigm was also used with chimpanzees (Gómez, 1994), and the results showed that subjects reacted to the test condition like typical children did: chimpanzees also looked directly to the experimenter's face upon the withdrawal of a reward.

Gómez (1991; 2004) claimed that one indicator of social understanding is that an individual views others as subjects rather than as objects. In his observations of an infant gorilla, Gómez noticed that when the gorilla led an experimenter to a door that needed opening, she looked directly into the experimenter's eyes and then alternated her gaze to the door and back to the experimenter's eyes again. If the gorilla were looking for a simply mechanical solution to her problem, Gómez argues, then she should have instead looked to other parts of the experimenter's body that were more directly related to the movements required to achieve the desired end, just as the children with autism in Phillips and colleagues' study (1992) did. In fact, Gómez found that the gorilla did exactly that in another situation: when the gorilla used the human as a climbing apparatus to reach the doorknob on her own. In this case, she

looked at the experimenter's body rather than his face. The difference in the gorilla's looking in these two circumstances could reflect an understanding of other individuals (in this case, humans) as subjects, rather than objects only.

A study with children with and without autism emerged from Gómez's (1991) experience with the infant gorilla. In this study, Phillips and colleagues (1995) placed desirable toys on a shelf, out of reach of the children. The child's first request for the toy, in whatever way this request occurred (e.g., verbal request, pointing) was ignored. Instead, the experimenter stood still and looked at the child's face. Any subsequent attempt to involve the experimenter was complied with suitably. The researchers claimed that failing to respond to the child's request would encourage the child to increase their effort to solve the problem, as previous research had showed that the likelihood of a child engaging in eye contact with an adult increases if that adult is initially unresponsive to the child (Bates et al., 1975). Phillips and colleagues found that children with autism engaged in significantly less eye contact and gaze alternation than typical children when reaching for or pointing toward the toy. It appeared that the typical children viewed the experimenter as a subject, but the children with autism did not.

In treating other individuals as subjects, rather than objects, non-human primates and normal children alternate their gaze between another individual's face and something of interest in the environment. Children with autism and primates attempting to achieve non-social means to an end do not exhibit the same pattern of face-directed looks. In the case of communication (as in the studies discussed above in which an individual needs help in achieving a desired end), face-directed looking may serve to provide information about the helper's attentional state. If the helper is not attending to the observer, then it is possible the helper will not fulfil the request

for help. In the section that follows, I discuss previous research that has explored whether non-human primates are able to modify their behaviour according the attentional states of others.

Tailoring behaviour to the attentional state of others

Manual gestures can only be effective when the recipient is able to perceive them (Bruner, 1975; Camaioni et al., 1976; Gómez, 1991). In order to engage appropriately in gestural communication, then, an individual should have an understanding of the attentional states of others, and should use gestures in a manner directly related to the attentional state of a recipient (Bruner, 1975; Tomasello, 1995). An individual should therefore gesture more when the recipient can see the gesture, and less (if at all) when the recipient cannot.

For example, Call and Tomasello (1994) showed that two orangutans gestured more often when a human experimenter was oriented toward them than when the experimenter's back was turned. One of these subjects, a highly enculturated individual named Chantek, also gestured more often when the experimenter's eyes were open than when the experimenter's eyes were closed. And Poss and colleagues (2006) found that gorillas and orangutans gestured more often when an experimenter was present than absent, and when an experimenter was oriented toward than away from the subject.

In their landmark study, Povinelli & Eddy (1996b) examined whether chimpanzees would modify their use of a begging gesture depending on the attentional state of a human experimenter. Chimpanzees were presented with two experimenters in each trial: one who could see the chimpanzee and one who could

not. Several experimental conditions were achieved by employing various postures (e.g., full body oriented toward versus away from the subject, head turned toward or away from the subject) and props (e.g., a bucket held over or just to the side of the experimenter's head, a blindfold covering the experimenter's eyes or mouth). From the start of the experiment, chimpanzees reliably chose the experimenter who could see them in the body orientation condition, a result corroborated by Hostetter and colleagues (2001); they found that chimpanzees used more manual gestures when a human experimenter was oriented toward them than when an experimenter had his back turned. Similarly, Krause and Fouts (1997) reported that chimpanzees waited until a human experimenter turned around to face them before pointing. However, in the other conditions of Povinelli and Eddy's study, chimpanzees chose randomly between experimenters. They reported that chimpanzees learned a "face rule" over time and, by the end of the experiment, they were thereby able to choose correctly in conditions where the presence of the experimenter's face could be used as a discriminative cue. Further, some subjects even learned an "eye rule" and so, over time, chose correctly when the presence of eyes could be used as a discriminative cue. Reaux and colleagues (1999) replicated this study a few years later with the same subjects to see if age played a role in performance. Perhaps, they reasoned, sensitivity to attentional states improved with development. Once again, chimpanzees chose correctly when choosing between an experimenter whose body was oriented forward and one whose back was turned. Chimpanzees showed a weak preference only for choosing correctly on those conditions to which a "face rule" could be applied, but improved over the course of the experiment, as in the original study.

Povinelli and Eddy (1996b) speculated that perhaps chimpanzees understand whether a human experimenter can or cannot see them, but are unable to use this

information in creating a gesture strategy. One important aspect of their study to consider, however, is that the experimenter to whom the chimpanzee should have gestured never looked directly at the chimpanzee's face in an effort to establish attentional contact. Instead, the experimenter merely made herself more attentionally available than the other by facing forward instead of away, or by not having a bucket over her head (Gómez, 2005a). If mutual attention is a key aspect of successful gestural communication, as has been suggested (Leung & Rheingold, 1981; Gómez, 1991; Desrochers et al., 1995; Leavens et al., 1996) then perhaps the choices presented to Povinelli and Eddy's chimpanzees were simply 'not good enough.' In fact, in another test condition run by Povinelli and Eddy (1996b), chimpanzee subjects used more gestures when an experimenter was making direct eye contact than when no mutual attention was established.

The results obtained by Povinelli and Eddy (1996b) do not end the story, however, as data from other labs provide conflicting insight into primates' understanding of attentional states. In a recent study by Bulloch and collaborators (2008), chimpanzees were tested using the same paradigm Povinelli and Eddy (1996b) used. However, the results obtained from their replication were different, as chimpanzees begged preferentially toward the experimenter who could see them right from the beginning of the experiment without having to learn this during the course of the experiment.

Furthermore, in everyday interactions, chimpanzees have been found to use purely visual gestures only when the recipient is attending to them, and use tactile signals when the recipient is attending elsewhere (Tomasello et al., 1994). These authors claimed that chimpanzees were using their gestures in a flexible way depending on how their gestures would be received by another individual. Further

evidence to support this claim comes from a more recent study in which Liebal and colleagues (2004) also reported that chimpanzees use more visually based gestures when the recipient is already attending to them. But what information is actually gained by the varying body and head orientations with which an ape is confronted? Is it information about that individual's attentional state, or some other behavioural cue?

In a study with chimpanzees, orangutans, and bonobos, Kaminski and colleagues (2004) measured in what ways apes are sensitive to body and face orientation by systematically crossing these two cues so that either could be oriented toward or away from the subject, creating four test conditions. They then measured apes' begging gestures in each condition and found that when the experimenter's body was oriented toward the subject, the subject used more gestures when the experimenter's face was also oriented toward the subject than when it was oriented away. However, when the experimenter's body was oriented away, apes' use of gestures did not change whether the experimenter's face was oriented toward or away from the subject. The results from Kaminski and colleagues' study stand in contrast to those of Povinelli and Eddy (1996b), as the subjects in Kaminski's study differentiated between an experimenter with her face oriented toward or away from them right from the beginning of the experiment, and did not need to learn a "face rule." However, apes' sensitivity to face orientation was limited to those cases in which the experimenter's body was oriented toward the subject, as they did not exhibit this sensitivity when the experimenter's body was oriented away. But why would chimpanzees use face orientation correctly in one instance but not in the other? The researchers proposed that apes could reason about the two cues in different ways: perhaps body orientation indicates an observer's likelihood to perform an action, but face orientation indicates an observer's 'perceptual access.' As such, apes should

gesture when a human experimenter can see them and is likely to respond, but not when an experimenter can see them but is unlikely to respond.

In addition to ape species, some monkeys have been studied to see whether they are also able to modify their behaviour based on the attentional states of a human experimenter. Hattori and colleagues (2007) found that capuchin monkeys were unable to do so. Although subjects spent more time looking at the face of an experimenter when the experimenter was looking at them, subjects did not point toward a food reward more often when the experimenter could see the gesture than when he could not. As capuchins did not engage in gaze alternation either (see previous section), the authors concluded that pointing lacked communicative function for capuchins and, instead, was strictly a result of training.

In a study with rhesus macaques, a species of Old World monkey that is more closely related to humans than capuchins are, Flombaum and Santos (2005) used a paradigm similar to that of Povinelli and Eddy (1996b), but within a competitive context. In their experiment, subjects chose from which of two experimenters to steal a piece of food, rather than request a piece of food. As in Povinelli and Eddy's study, one experimenter could see the subject while one could not, due to the use of varying body postures and barriers. The data revealed that, in all conditions, subjects spontaneously stole food from the experimenter who could not see them. One possible explanation for these results is the "evil eye" hypothesis described, and then tested for, in an experiment with chimpanzees by Hare and colleagues (2001). Under this hypothesis, a subordinate avoids any food that has been seen by a more dominant individual, even if the dominant individual cannot see it at that time, as if the item were marked as forbidden by the dominant's gaze. Hare and colleagues found that the evil eye hypothesis did not apply to chimpanzees. Subordinate individuals readily

approached and took food a dominant individual had previously seen placed in one hiding spot, but had then been moved to a new location when the dominant individual could not see. If the food had been 'tainted' by the dominant's gaze to begin with, the subordinate would not have approached the food at all. In the case of Santos and colleagues' (2005) rhesus macaques, both human experimenters faced forward to begin the trial, and thereby saw the food. If the evil eye hypothesis were at work here, subjects should have chosen randomly between the experimenters no matter their attentional state seconds later, or would not have approached at all. This was not the case, as subjects did approach and preferred to steal from the experimenter who could not see them.

While some studies report conflicting results, there is convincing evidence that apes and monkeys are able to recognise the attentional states of another individual and respond appropriately, especially given the right experimental conditions. It would be informative to integrate the two topics discussed above – face-directed looking and the modification of behaviour based on another individual's attentional state – in one study. In this way we can properly explore how these two phenomena might interact and, as a result, obtain further insight into the role face-directed looking plays in primate behaviour.

Gaze alternation use and attentional states

Gaze alternation and other visual attention strategies associated with social referencing can serve many purposes. In ambiguous situations, visually referring to another individual can provide information useful in evaluating objects or events or in determining another individual's intentions. Face-directed looking can also serve a

communicative function, as these looks can be an attempt to engage in mutual attention or can simply allow an individual to check whether another has seen its actions. As prosimian species have been overlooked in studies exploring this behaviour, it is unclear at what point in primate evolution the ability to use these looking strategies emerged. Is it a simian trait or is the origin much earlier, so including prosimian species? And does the ability to modify one's behaviour based on what was observed extend to prosimian species as well?

In order to explore whether lemurs use face-directed looking, I found the paradigm used by Phillips and colleagues (1992) to be a good starting point. This paradigm allowed me to ask whether lemurs check for social information when presented with an ambiguous interaction, and also provided an opportunity for modification to explore differential use of face-directed looking. I presented lemurs with three different types of test trials, in each of which I exhibited a different attentional state. In this way I was able to determine whether lemurs looked to my face for social information, and also explore how they used the information once they gathered it. If lemurs alternated their gaze differently according to my attentional state, it would provide clues as to the function of gaze alternation for these animals. In an unexpected development, lemurs used their trained pointing gesture in this context, a paradigm different from those in which they had used the gesture previously. As such, I was also able to measure whether their pointing also varied depending on my attentional state.

4.1 – Experiment 1: Teasing

4.1.1 – Method

Subjects

Subjects were four brown lemurs (Hyacinthe, Hutch, Honorine, and Hermine) and two black lemurs (Rousse and Rustine) at the Centre de Primatologie, as described in Chapter 2.

Procedure

I sat on the floor facing the subjects' home enclosure and waited for the subject to position itself directly in front of me. I maintained a neutral expression while looking straight ahead and held a raisin close to my body at chest-level. To begin the trial, I extended my arm to bring the raisin to the subject's mouth. In Baseline trials, I allowed the subject to consume the raisin and then returned my hand to the starting position. In Test trials, I retracted the reward just as the subject was about to eat it, returned my hand (which was still holding the raisin) to the starting position, and adopted one of three attentional states:

Subject – I oriented my head and eyes toward the subject's face.

Object – I oriented my head and eyes toward the raisin I held in my hand.

Away – I oriented my head and eyes up into the corner created by the wall and the wire mesh separating the room and the enclosure.

After five seconds, I extended my arm toward the subject and allowed it to consume the raisin.

Sessions consisted of twenty trials, sixteen of which were Baseline trials, four of which were Test trials. Test trials were interspersed within sessions so that at least two Baseline trials occurred between them. Test trial types were administered randomly. Subjects completed twelve sessions each, giving sixteen trials in each of the test conditions.

Behavioural analysis

In their study, Phillips and colleagues (1992) recorded the number of trials in which children looked to the experimenter's face and compared, between conditions, the number of individuals who did so in at least 50% of trials. I employed a stricter criterion for my experiment: instead of recording the number of trials in which subjects looked to my face at all, I recorded the number of trials in which subjects looked to my face *first*. For Test trials, this look was the first shift in attention after I took the raisin away. For Baseline trials, this look was the first shift in attention after I allowed them to take the raisin from me.

I also coded video for how much time elapsed between the beginning of the trial and the subject's first look to my face, recorded the total time subjects spent looking at my face during each trial, and recorded the length of each face-directed look.

In addition, I noted the sequence of subject's visual inspections throughout the course of each test trial in order to explore gaze alternation. Gaze alternation has been

defined in different ways. In some studies, researchers have treated as behaviourally significant any sequences of two looks that were directed to an object of interest and then to another individual (or vice versa) (Russell et al., 1997; Leavens & Hopkins, 1998; Leavens et al., 2004). However, other researchers (Klinnert, 1984; Sorce et al., 1985; Anderson et al., 2007) instead focused only on sequences consisting of three looks between an object of interest and another individual (e.g., object – face – object). And yet other researchers explore gaze alternation, but do not provide criteria (Leavens et al., 1996; Hattori et al., 2007). I chose the most robust of these criteria, defining gaze alternation as a sequence of at least two looks (face – object or object – face, Figure 4.1), but I also took note of how many looks between the object (the raisin) and my face occurred before lemurs looked elsewhere. I called this number the length of the gaze alternation bout, and I analysed these data to see whether longer strings occurred, and whether bout length varied across conditions. In addition, I recorded the total number of gaze alternation bouts for each trial. I feel this approach satisfies both the competing approaches to gaze alternation analysis.

During the course of the study, I noticed that subjects indicated toward the raisin I had withdrawn using a gesture they had been trained to use for indication in an unrelated context (hereafter: pointing; see Chapter 2). I decided to measure this behaviour across conditions. I recorded how many times subjects pointed and how much time elapsed between the beginning of the trial and subjects' first point. I considered the beginning of a point to be when the lemur's arm was extended through the wire mesh past the wrist. Further, just as Hattori et al (2007) had done, I did not require the arm to fully retract, but did require the subject to pull back its arm slightly, before coding a new point. The backward movement of the arm for more than two frames (0.16 seconds) indicated this distinction, and a new point was recorded as

Figure 4.1 – Gaze alternation example. Stills from a test trial with Rousse (Ro) exhibiting (from left to right) a look to my face, a look toward the raisin reward ('object'), and another look to my face.

having begun when the arm began forward motion once again. If lemurs understand the communicative nature of this trained gesture, then they should be sensitive to my attentional state and thereby indicate more often in the Subject condition, as that was when mutual attention was established, than in the Away and Object conditions, in which there was no mutual attention between the subject and me. Another possibility, however, is that lemurs understand that their gesture must be perceived in order to produce the desired outcome, without understanding the communicative function of attentional contact. In this case, lemurs should gesture more in the Subject and Object conditions, when their gesture could possibly have been seen, than in the Away condition, when it was impossible for me to see their gesture.

In order to assess inter-observer reliability, an experimenter not associated with the study coded 10% of trials (N=29). Pearson's correlations revealed a high level of agreement for latency to looking at the experimenter's face (r=0.78, P=0.01), time spent looking at the experimenter's face (r=0.72, P=0.015), the length of gaze alternation bouts (r=0.68, P=0.02), the number of gaze alternation bouts (r=0.67, P<0.001), the latency to lemurs' first points (r=1.00, P<0.001), and the number of points (r=1.00, P<0.001).

4.1.2 – Results

Looking

If lemurs seek out social information when confronted with an ambiguous situation, they should first look to my face more often in the Test than in the Baseline condition. Six out of six subjects first looked to my face in at least 50% of trials in the Test condition, while only one out of six lemurs did so in the Baseline condition (Figure 4.2a). By using non-parametric analyses, with each subject's percentage score as a data point, I found that all six subjects looked to my face at the trial start in a greater number of Test than Baseline trials (Wilcoxon signed ranks test; z= -2.20; P=0.028; Figure 4.2b).

I went on to explore the latency to subjects' first face-directed look in Baseline and Test trials. I predicted that lemurs should look to my face more quickly in Test trials (the ambiguous situation) than in Baseline trials (the unambiguous situation). Four out of six subjects did so (Mann-Whitney U; Hy: U=419.0, N1=48, N2=47, P<0.001; Hu: U=444.5, N1=48, N2=42, P<0.001; Ho: U=551.5, N1=48, N2=40, P=0.001; He: U=610.5, N1=48, N2=33, P=0.08; Ro: U=617.5, N1=48, N2=37, P=0.016; Ru: U=150.0, N1=28, N2=16, P=0.13; Figure 4.3).

Separating test trials into Subject, Away, and Object conditions, I analysed the total amount of time subjects spent looking at my face per trial in the Test condition, as well as the length of each face-directed look. If lemurs were engaging in mutual attention, they would look to my face longer in the Subject condition than in both the

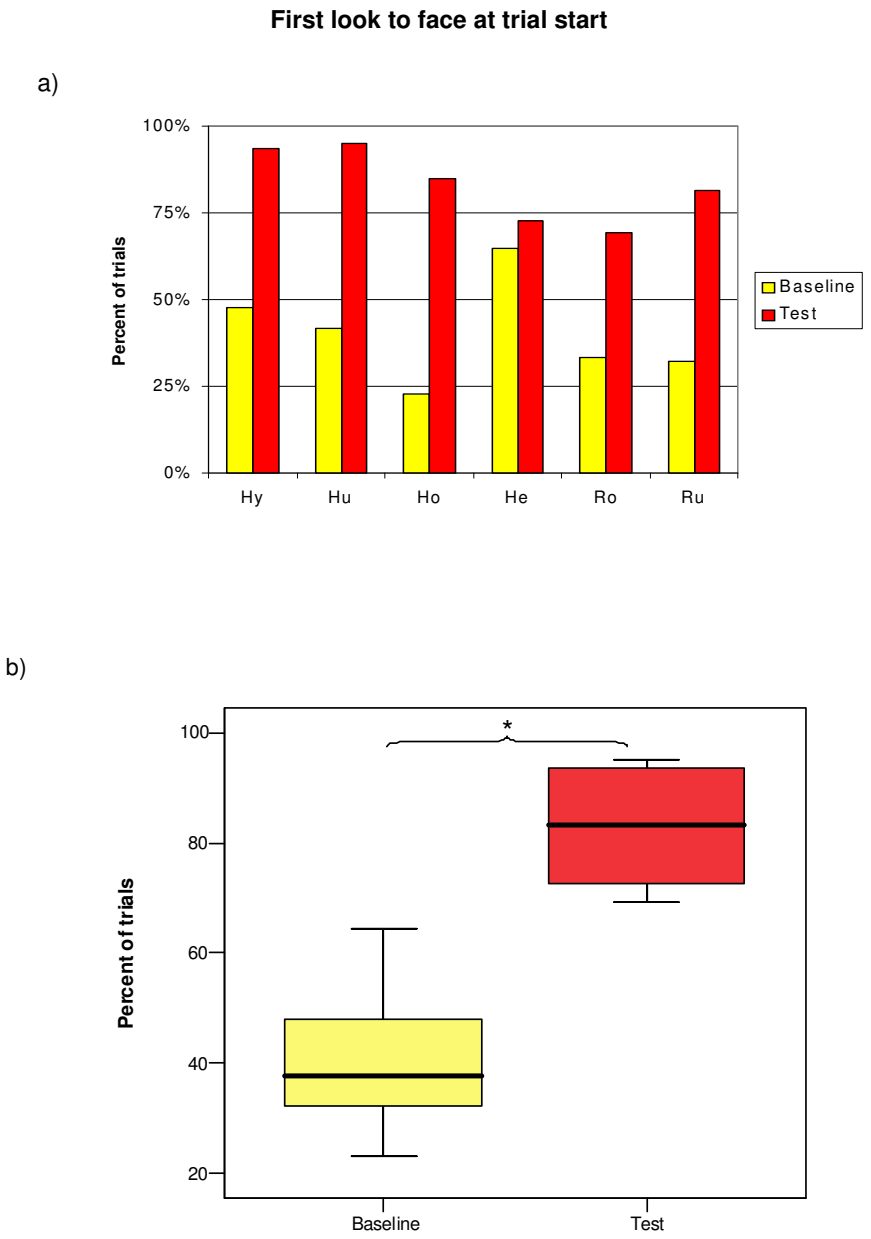

Figure 4.2 – a) First look to face at trial start. The percent of trials in which each subject first looked to my face after the beginning of the trial in both the Baseline and Test condition. b) Using each subject's percentage score as a data point, the percent of trials in which the group looked to my face first after the beginning of a trial in both the Baseline and Test conditions. Bold lines represent the median percentage, the boundaries of each box represent the inter-quartile range. Whiskers represent the range. Wilcoxon signed ranks test: * $P<0.05$

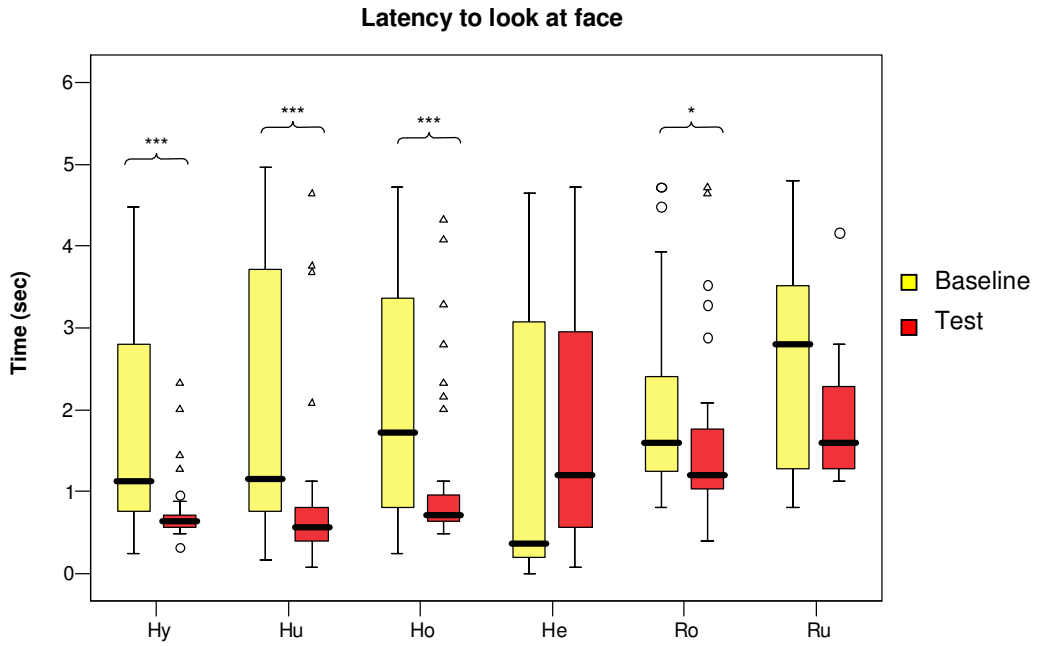

Figure 4.3 – Latency to look at face. The time between the beginning of a trial and each subject's first look directed at my face in Baseline and Test trials. Bold lines represent the median latency; the boundaries of each box represent the inter-quartile range. Whiskers represent the range, while outliers are marked by circles and triangles. Mann-Whitney U test - *** $P \leq 0.001$, * $P < 0.05$

Away and Object conditions. If referring to my face served another purpose, such as simply monitoring my attention as a way to predict food delivery, then looking time would not differ across conditions. To ensure that any looking time differences were a result of my attentional state, I did not include trials in which subjects did not look to my face at all. Only one subject, Hyacinthe, showed a significant difference in total looking time (ANOVA; Hy: F=5.06, df=2, P=0.011; Hu: F=2.44, df=2, P=0.10; Ho: F=2.66, df=2, P=0.083, He: F=1.64, df=2, P=0.21; Ro: F=1.94, df=2, P=0.16; Figure 4.4), and Tukey post-hoc tests conducted for that individual showed that she looked longer in the Subject than in the Object condition (Hy: P=0.010). As Rustine only

looked to my face once in the Away condition, no average for this condition could be calculated. I was able to compare average looking times for this individual in the Subject and Object conditions using a *t*-test and found that she looked at my face significantly longer in the Subject than in the Object condition (Ru: t=2.24, df=12, P=0.044). Two subjects, Hyacinthe and Honorine, exhibited a significant difference in the average length of face-directed looks across conditions (ANOVA; Hy: F=4.80, df=2, P=0.010; Hu: F=0.88, df=2, P=0.42; Ho: F=5.13, df=2, P=0.010; He: F=2.74, df=2, P=0.075; Ro: F=2.33, df=2, P=0.11; Figure 3.5). Tukey post-hoc tests showed that Hyacinthe's individual looks were longer in the Subject than in the Object condition (Hy: P=0.008) and Honorine's individual looks were longer in the Away than in the Object condition (Ho: P=0.007). Again, as Rustine exhibited only one face-directed look in the Away condition, no average for this condition could be calculated. I compared the average length of face-directed looks in the Subject and Object conditions using a *t*-test. I found that Rustine's face-directed looks were longer in the Subject than in the Object condition (Ru: t=2.25, df=12, P=0.044).

With no strong pattern emerging in lemurs' looking time, I went on to explore lemurs' use of gaze alternation. All subjects engaged in gaze alternation in all conditions, but, when comparing the average number of gaze alternation bouts per trial, no clear patterns emerged. Only one subject, Rustine, showed a significant difference in its average number of gaze alternation bouts across conditions (ANOVA; Hy: F=0.30, df=2, P=0.74; Hu: F=0.81, df=2, P=0.45; Ho: F=1.81, df=2, P=0.18; He: F=1.88, df=2, P=0.16; Ro: F=3.03, df=2, P=0.058; Ru: F=4.21, df=2, P=0.02; Figure 4.6). Tukey post-hoc tests conducted for this subject revealed that she engaged in more gaze alternation in the Subject than in the Away condition (Ru: P=0.019).

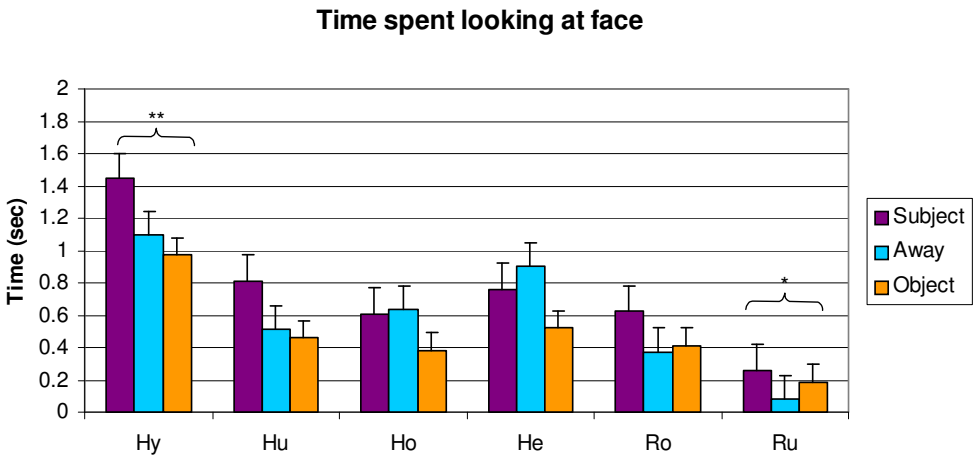

Figure 4.4 – Time spent looking at face. For each subject, the average amount of time it spent looking at my face during the course of a trial in each of the three Test conditions. For Hy, Tukey post-hoc Test: ** P=0.01. For Ru, independent t-test: * P<0.05.

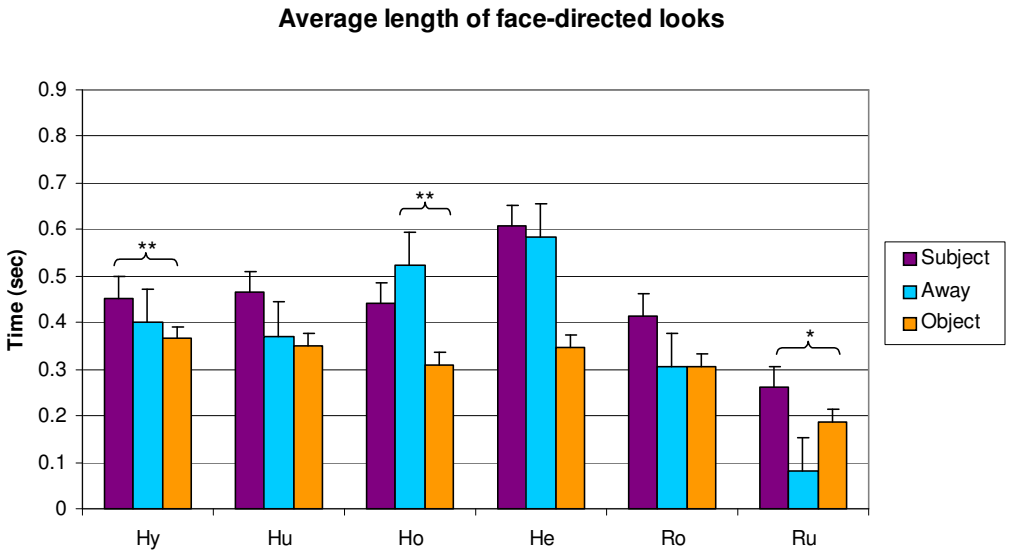

Figure 4.5 – Average length of face-directed looks. For each subject, the average amount of time spent looking at my face each time they looked in each of the three Test conditions. Tukey post-hoc test: ** P<0.01. For Ru, independent t-test: * P<0.05

I went on to determine whether the length of gaze alternation bouts varied across test conditions. Only one subject engaged in different bout lengths across conditions (ANOVA; Hy: F=2.70, df=2, *P*=0.073; Hu: F=4.00, df=2, *P*=0.025; Ho: F=1.32, df=2, *P*=0.28; He: F=1.46, df=2, *P*=0.25; Ro: F=0.96, df=2, *P*=0.39; Figure 4.7) and Tukey post-hoc tests revealed that this subject exhibited longer sequences in the Subject than in the Object condition (Hu: *P*=0.027). As Rustine only engaged in one bout of gaze alternation in the Away condition, no average for this condition could be calculated. I went on to compare her behaviour in the Subject and Object conditions using a *t*-test, but she did not exhibit any difference in gaze alternation length between these conditions (Ru: *t*=0.62, df=11, *P*=0.55).

Pointing

I analysed the occurrence of gestures between test conditions to see if lemurs' use of their trained pointing gesture varied depending on my attentional state. Lemurs did not show any significant differences between conditions in the percent of trials in which they pointed (Chi-squared test: Hy: X^2=0.17, df=2, *P*=0.92; Hu: X^2=0.20, df=2, *P*=0.91; Ho: X^2=1.53, df=2, *P*=0.47; He: X^2=0.53, df=2, *P*=0.97; Ro: X^2=1.08, df=2, *P*=0.58; Ru: X^2=0.50, df=2, *P*=0.78; Figure 4.8). I also examined the average number of pointing gestures per trial, using a Kruskal-Wallis test given the skew of the data, and once again found no significant differences between conditions for any subject (Hy: H=4.51, df=2, *P*=0.11; Hu: H=0.25, df=2, *P*=0.88; Ho: H=2.57, df=2, *P*=0.28; He: H=0.86, df=2, *P*=0.65; Ro: H=1.15, df=2, *P*=0.56; Ru: H=0.73, df=2, *P*=0.69; Figure 4.9)

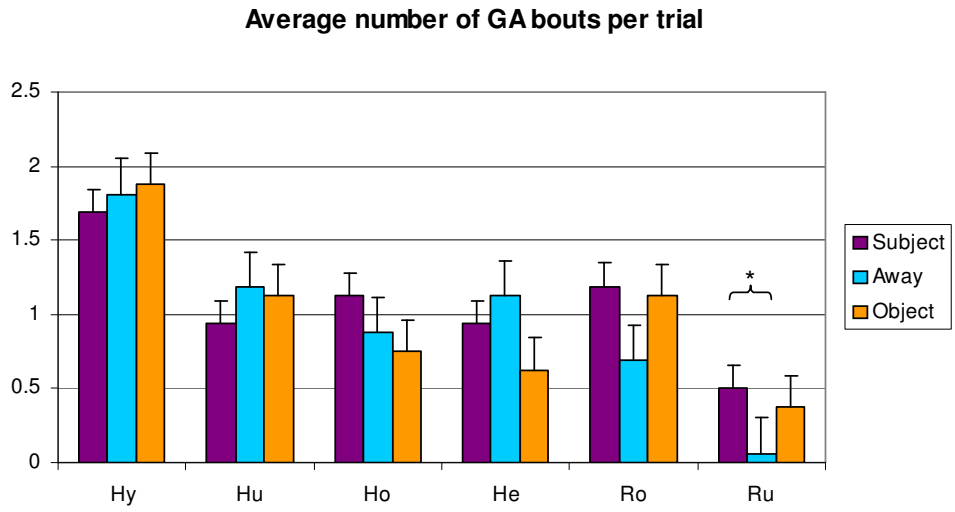

Figure 4.6 – Average number of gaze alternation bouts per trial for Experiment 1. Data presented by subject, separated into the three Test conditions. Whiskers represent standard error of the mean. Tukey post-hoc tests: * $P<0.05$

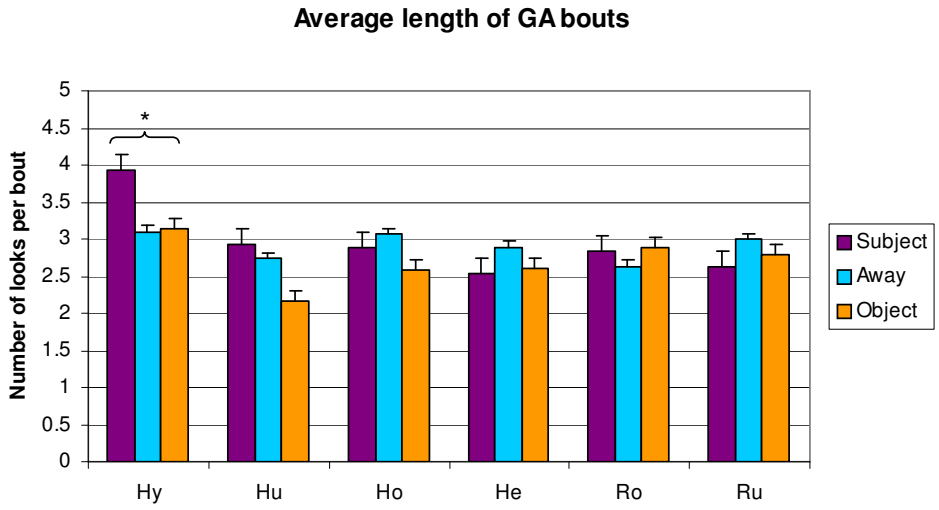

Figure 4.7 – Average length of gaze alternation bouts for Experiment 1. The average number of looks occurring in each gaze alternation bout exhibited by each subject in each Test condition. Whiskers represent standard error of the mean. Tukey post-hoc tests: * $P<0.05$

I recorded each subject's latency to first exhibit a pointing gesture in all trials to see if subjects used the gesture more quickly when I could see them. Trials in which lemurs did not point were not given a score and were removed from analysis. Given the skewed nature of the data, I conducted the non-parametric Kruskal-Wallis statistic to compare latencies in each test condition. Five out of six subjects did not exhibit significant differences (Hy: H=2.87, df=2, *P*=0.24; Hu: H=0.94, df=2, *P*=0.62; Ho: H=3.32, df=2, *P*=0.19; Ro: H=0.88, df=2, *P*=0.64; Ru: H=2.78, df=2, *P*=0.25; Figure 4.10). One subject, Hermine, did show a significant difference in latency (He: H=14.8, df=2, *P*=0.001), and Mann-Whitney U tests revealed that she was faster to point in the Subject condition than in both the Away condition (U=17.5, z=-3.30, *P*<0.001) and Object condition (U=20.0, z=-3.31, *P*<0.001).

4.1.3 – Discussion

Povinelli and Eddy (1996b) have argued that training a primate to point is no different than training that individual to perform some arbitrary behaviour (e.g., scratching its elbow) in order to receive a reward. As a result, the primate is unlikely to understand the communicative nature of the gesture. However, some primates spontaneously look to an experimenter's face when using a trained gesture (Blaschke & Ettlinger, 1987; Gómez, 2005a), which is exactly what I found with lemurs in this experiment. Though they were trained to indicate choices of stimuli by abbreviated reaching, they were not trained to engage in gaze alternation with a human experimenter. Yet, all subjects did it. What, then, is the purpose of their gaze alternation?

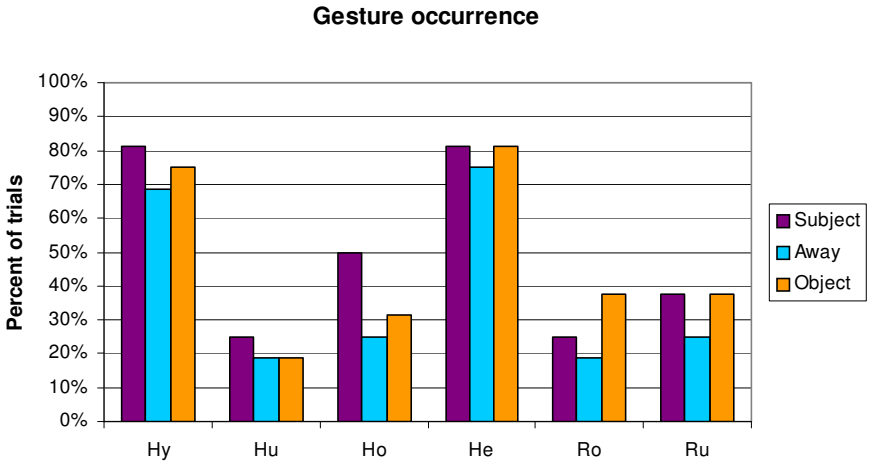

Figure 4.8 – Gesture occurrence. Percent of trials, per condition, in which each subject pointed at least once.

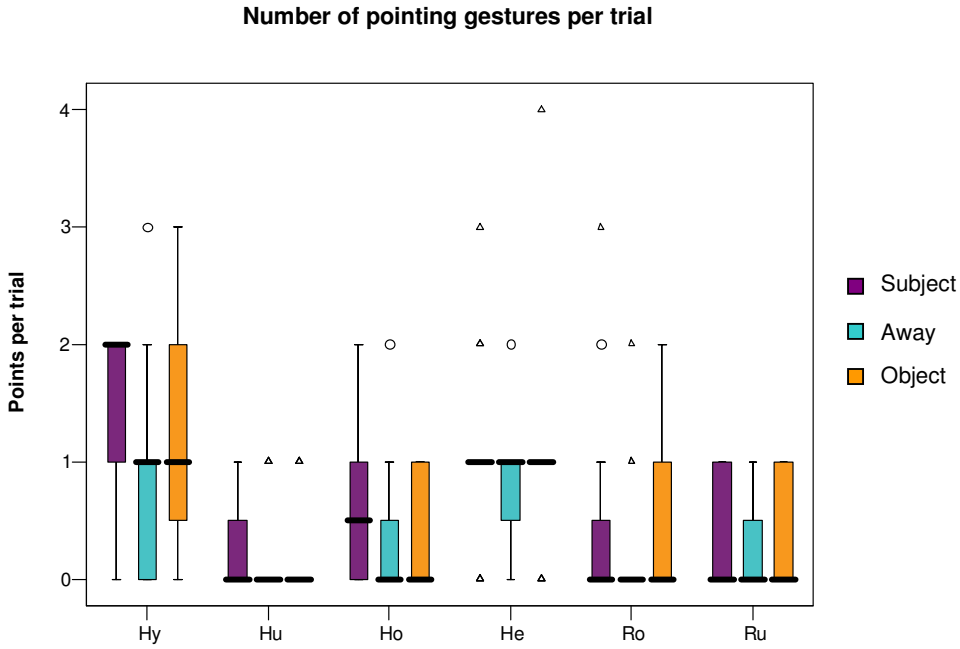

Figure 4.9 – Number of pointing gestures per trial for Experiment 1. The average number of times each subject pointed per trial in each of the Test conditions. Bold lines represent the median number of points; the boundaries of each box represent the inter-quartile range. Whiskers represent the range, while outliers are marked by circles and triangles. No significant differences were found.

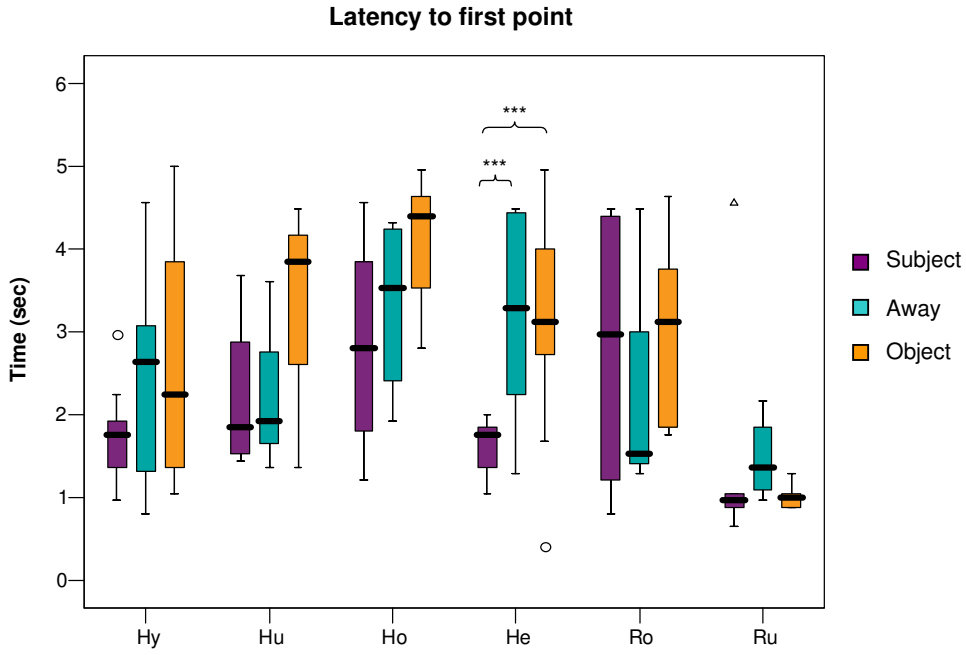

Figure 4.10 – Latency to first point. For each subject, the time between the beginning of the trial and the first pointing gesture exhibited in that trial in all three Test conditions. Bold lines represent the median latency; the boundaries of each box represent the inter-quartile range. Whiskers represent the range, while outliers are marked by circles and triangles. Mann-Whitney U test: *** $P \leq 0.001$

Perhaps lemurs were seeking a social explanation to their problem (not receiving the raisin that they were about to get). If they sought a mechanical solution for the delay in receiving the raisin in the Test condition, they should have focused on my hand, or even my arm, without paying much attention to my face at all. This response would have been akin to that of Gómez's gorilla when she pushed an experimenter toward a door and then used him as a climbing aid in order to reach the doorknob (1991) and to that of the children with autism in Phillips and colleagues' study (1992), which used the paradigm from which my experiment was developed. Instead, I found that lemurs quickly looked to my face after the food was pulled away

from them, and frequently referred to my face until the food was returned, just as the gorilla Gómez observed did later in her development, when she led the experimenter to the door instead of pushing him there, and as the typical children did in the experiment by Phillips and colleagues (1992).

Despite lemurs' decreased latency to looking at my face in the Test condition and their tendency to look to my face first more often in the Test condition than in the Baseline condition, their looking behaviour did not change according to what they saw. That is, their face-directed looking did not vary according to my attentional state. Though there are a few instances in which a subject engaged in significantly more gaze alternation or spent more time looking at my face when mutual attention was established and no instances in which subjects did so in the other conditions, there was no strong or clear pattern across conditions for any of the measures used.

Gaze alternation is given great importance in the child development literature because a gesture is effective in the first place only if the recipient perceives it, and checking the face of the recipient could be an indication that the signaller understands something about the link between gestures and attention. Gómez (1991) interpreted the looks made to an experimenter's face by a gorilla that wanted a door to be opened as checks to see whether the experimenter was attending to her actions. Gómez argued that, when an individual is making a request of another, it is essential for him to know if his request is being perceived by the potential helper, as perceiving is causally related to acting. Perhaps, then, the unclear pattern of gaze alternation occurrence between test conditions makes sense: when a request is being made, the requester must monitor whether the helper is attending until the request is fulfilled. However, despite lemurs' frequent looks to my face, they did not modify their pointing based on

my attentional state. If lemurs looked to my face for attention checking, then there should have been behavioural differences based on what they found.

Povinelli & Eddy (1994) suggested that gaze alternation, instead, might just be a pattern of looking between two objects that interest an individual greatly, rather than an indication that the individual understands attention. They do admit, however, that gaze alteration could also indicate an understanding that the face provides cues useful in behaviour prediction, in an animal that lacks understanding of mental states. In other words, lemurs could have checked my face for a cue that they were about to receive food or that I was keeping it for myself, rather than to check whether I was attending to them. These cues could include a threatening facial expression or putting the raisin into my mouth to eat it myself.

While a look to the face of an observer during gesturing is often cited as one symptom of an intentionally communicative gesture (Bates, 1976; Camaioni et al., 1976; Bates, 1979; Bruner, 1981; Leung & Rheingold, 1981; Gómez, 1991; Leavens et al., 1996; Leavens & Hopkins, 1998; Leavens & Hopkins, 1999), the lemurs did not modify their gesture use based on what they saw after looking at my face. Perhaps, though, factors unrelated to their socio-cognitive abilities were at play that affected lemurs' use of their trained gesture. These individuals were trained to point to food placed onto a pivoting platform by a human experimenter, who would immediately rotate the platform toward the subject after it had pointed. The conditions of Experiment 1 were different to those in which lemurs were originally trained to point. Perhaps the distractive nature of a novel situation in which they'd never before used the gesture affected their ability to integrate properly their behaviour with the social information they had gathered by using gaze alternation. I decided, then, to conduct a second experiment more akin to the context in which the lemurs had been trained in

order to explore whether they would modify their use of pointing given my attentional state under more familiar conditions.

4.2 – Experiment 2: Delayed reward

As subjects were trained to point to food items placed on a platform, I used this method to once again examine whether they would modify their gesture use according to my attentional state. The study conducted with children with and without autism by Phillips and colleagues (1995), in which an experimenter placed a toy out of reach of the subject and did not respond to his initial requests for the toy, provided a simple way to incorporate a familiar situation for the lemurs while allowing a way to induce attention-checking. The procedure used by Phillips and colleagues (1995), in which an experimenter is temporarily unresponsive to a subject, has become standard in testing non-human animals for gesture modification and spontaneous social attention (e.g. Call & Tomasello, 1994; Hostetter et al., 2001; Povinelli et al., 2003; Kaminski et al., 2004; Xitco et al., 2004; Poss et al., 2006; Anderson et al., 2007; Hattori et al., 2007). For the experiment that follows, I placed a raisin on a platform that was out of reach for the lemur subjects. When lemurs pointed to the raisin, I most often responded by moving the platform closer to the lemurs so they could retrieve the food reward. In test trials I delayed my response to their gesture and used these delays to take on varying attentional states. In this way, I was able to analyse lemurs' use of pointing in a context more similar to that in which they were trained to use the behaviour.

4.2.1 – Method

Subjects

Subjects were the same individuals that participated in Experiment 1: four brown lemurs (Hyacinthe, Hutch, Honorine, and Hermine) and two black lemurs (Rousse and Rustine), as described in Chapter 2.

Procedure

A pivoting platform (70 X 16 X 25 cm) was situated in front of the wire mesh of the lemurs' home enclosure so that a lemur could not reach the apparatus with a fully extended arm. I sat on the floor behind the platform and facing the enclosure and waited for the subject to position itself directly in front of me.

I maintained a neutral expression while looking straight ahead and placed a raisin on one side of the platform. The subject then indicated toward the raisin, as all had been trained to do previously (see Chapter 2). In Test trials, I did not immediately respond to their gesture, and instead adopted one of three attentional states:

Subject – I oriented my head and eyes toward the subject's face.

Object – I oriented my head and eyes toward the raisin on the platform.

Away – I oriented my head and eyes up into the corner created by the wall and the wire mesh separating the room from the enclosure.

After five seconds, I pulled toward myself the side of the platform opposite to the raisin, which brought the side containing the raisin to the subject. As the platform was now rotated so that lemurs could easily grasp the raisin, they reached through the mesh and retrieved the reward. In between Test trials, I added several filler trials in which I immediately responded to subjects' first point in order to prevent frustration and participation refusal.

Sessions consisted of twenty trials, sixteen of which were filler trials, four of which were Test trials. Test trials were interspersed throughout the session so that at least two filler trials occurred between them. Test trial types were administered randomly. Each subject completed between eleven and twelve sessions (variation was due to participation differences), totaling between fourteen and sixteen trials in each of the test conditions.

The predictions for this experiment were the same as those made in Experiment 1. If lemurs understand the importance of a recipient's attentional state, they should gesture differentially between test conditions: gesturing more when I was attending to them and less when I was not.

Behavioural analysis

As in Experiment 1, I analysed lemurs' looking by recording the occurrence of gaze alternation as well as the length of individual gaze alternation bouts (see Experiment 1 Methods).

In addition to the measures I used to explore pointing in Experiment 1 (average number of points per trial and latency to lemurs' first point after the trial began), I also measured the inter-gesture interval. This was the amount of time

between the end of one gesture and the beginning of the next, for all gestures in a trial. Lemurs might use gestures in quick succession when mutual attention is established or when I can see them, as the communicative effort would be effective. Or, lemurs might exhibit response waiting under these conditions, as one perceived gesture should be enough to elicit a response (Bruner, 1981; Tomasello et al., 1985).

To asses inter-observer reliability a secondary coder not associated with the experiment analysed 10% of trials (N=25). Pearson's correlations revealed a high level of agreement for the number of gaze alternation bouts (r=0.64, P=0.014), the length of gaze alternation bouts (r=0.65, P=0.02), the number of points (r=0.75, P=0.006), and the inter-point interval (r=0.69, P=0.018).

4.2.2 - Results

Looking

As in Experiment 1, I analysed the average number of times per trial subjects engaged in gaze alternation. As in the previous experiment, all subjects engaged in gaze alternation. However, only two subjects exhibited a difference in the average number of gaze alternation bouts per trial across conditions (ANOVA; Hy: F=2.69, df=2, P=0.079; Hu: F=2.01, df=2, P=0.15; Ho: F=3.82, df=2, P=0.030; He: F=0.35, df=2, P=0.71; Ro: F=1.79, df=2, P=0.18; Ru: F=5.00, df=2, P=0.011; Figure 4.11). Tukey post-hoc comparisons show Honorine engaged in more bouts of gaze alternation per trial in the Subject condition than in the Object condition (Ho: P=0.023), while Rustine engaged in a greater number of gaze alternation bouts in the

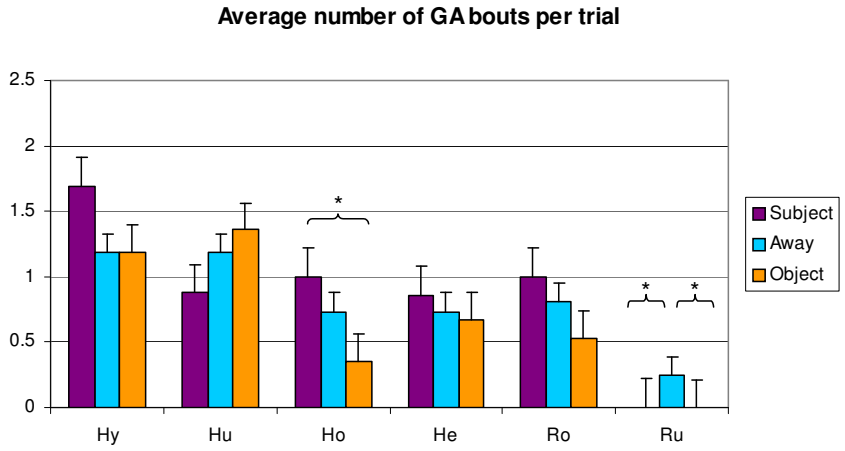

Figure 4.11 – Average number of gaze alternation bouts per trial for Experiment 2. Data presented by subject, separated into the three Test conditions. Whiskers represent standard error of the mean. Tukey post-hoc tests: * $P<0.05$

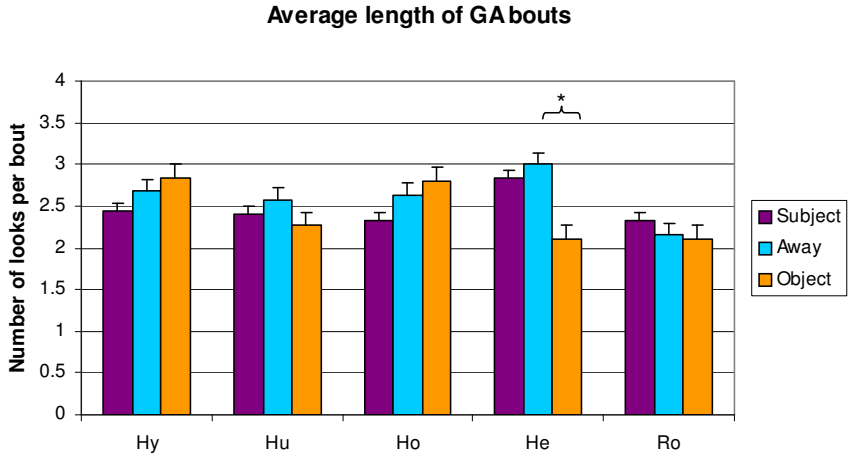

Figure 4.12 – Average length of gaze alternation bouts for Experiment 2. The average number of looks occurring in each gaze alternation bout exhibited by each subject in each Test condition. Whiskers represent standard error of the mean. Tukey post-hoc tests: * $P<0.05$

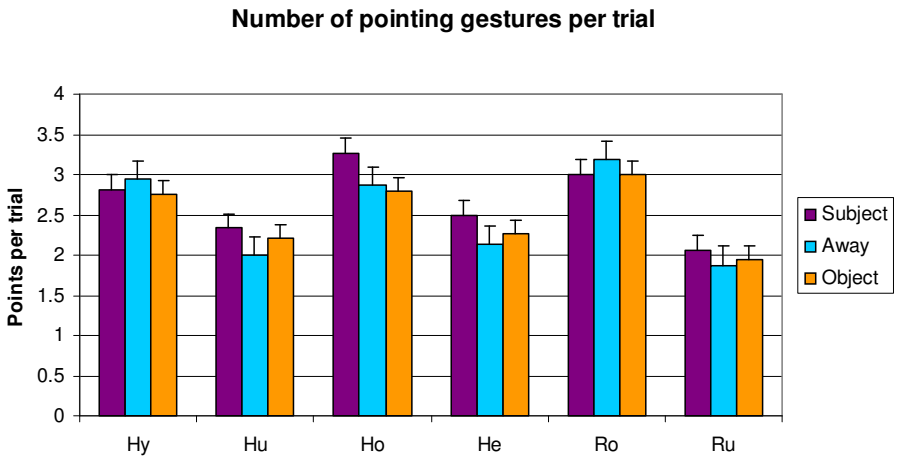

Figure 4.13 – Number of pointing gestures per trial for Experiment 2. The average number of times each subject pointed per trial in each of the Test conditions. Whiskers represent standard error of the mean. No significant differences were found.

Away condition than both the Object (Ru: *P*=0.023) and the Subject (Ru: *P*=0.023) conditions.

I also calculated the average length of gaze alternation bouts for each subject in every condition. As Rustine engaged in gaze alternation in the Away condition only, cross-condition comparisons of bout length could not be made for her. Only one of the remaining five subjects exhibited a significant difference in length (ANOVA; Hy: F=0.80, df=2, *P*=0.45; Hu: F=1.33, df=2, *P*=0.27; Ho: F=2.23, df=2, p=0.13; He: F=3.48, df=2, *P*=0.044; Ro: F=1.022, df=2, *P*=0.37; Figure 4.12). Tukey post-hoc tests reveal that this individual's gaze alternation bouts were longer in the Away condition than in the Object condition (He: *P*=0.048).

Pointing

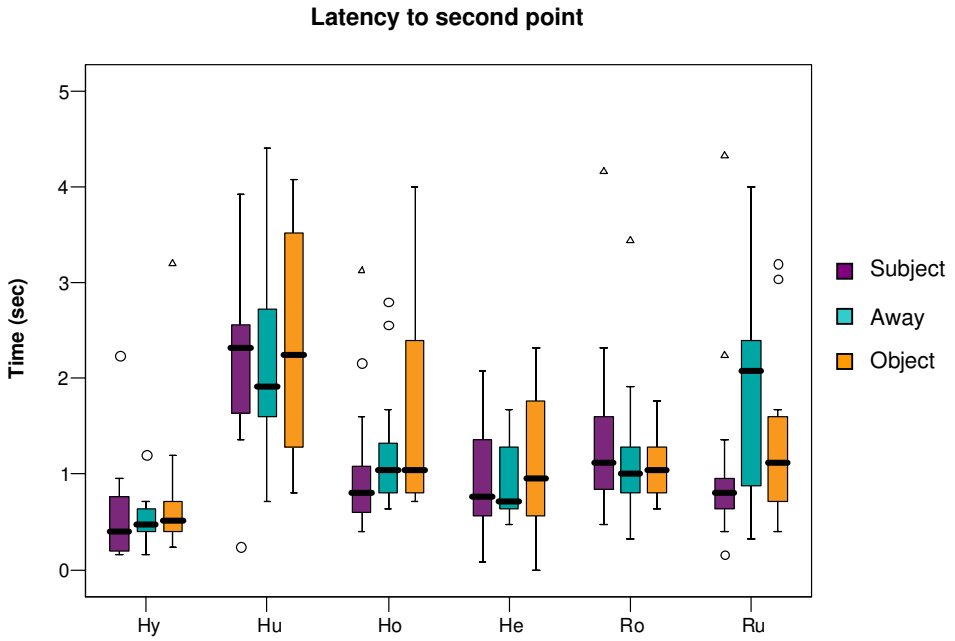

Figure 4.14 – Latency to second point. For each subject, the time between the end of the first pointing gesture used and the second for all three Test conditions. Bold lines represent the median latency; the boundaries of each box represent the inter-quartile range. Whiskers represent the range, while outliers are marked by circles and triangles. No significant differences were found.

To see whether subjects' use of pointing varied depending on my attentional state, I compared the average number of points per trial between conditions for each individual. No subject exhibited a significant difference (ANOVA; Hy: F=0.27, df=2, *P*=0.77; Hu: F=1.11, df=2, *P*=0.34; Ho: F=1.29, df=2, *P*=0.29; He: F=0.92, df=2, *P*=0.41; Ro: F=0.41, df=2, *P*=0.66; Ru: F=0.33, df=2, *P*=0.72; Figure 4.13).

I also investigated whether there was a difference in how long lemurs waited before pointing for a second time by measuring the time between the end of the initial point, which started the trial, and the beginning of the next point. Trials in which lemurs did not point again were not given a score and were removed from analysis. These data were skewed, and so I performed non-parametric statistics. No significant differences were found for any subject (Kruskal-Wallis; Hy: H=1.28, df=2, *P*=0.53;

Hu: H=0.23, df=2, *P*=0.89; Ho: H=3.85, df=2, *P*=0.15; He: H=0.93, df=2, *P*=0.63; Ro: H=0.82, df=2, *P*=0.67; Ru: H=4.60, df=2, *P*=0.10; Figure 4.14). I further explored how long lemurs waited before gesturing by comparing the inter-gesture interval for all gestures in each trial. This set of data includes not only the time between the first and second gestures, but also the time between the second and third, third and fourth, etc. Once again, no significant differences were found for any subject (Kruskal-Wallis; Hy: H=1.10, df=2, *P*=0.58; Hu: H=0.28, df=2, *P*=0.87; Ho: H=4.66, df=2, *P*=0.10; He: H=0.27, df=2, *P*=0.87; Ro: H=0.22, df=2, *P*=0.89; Ru: H=3.40, df=2, *P*=0.18; Figure 4.15).

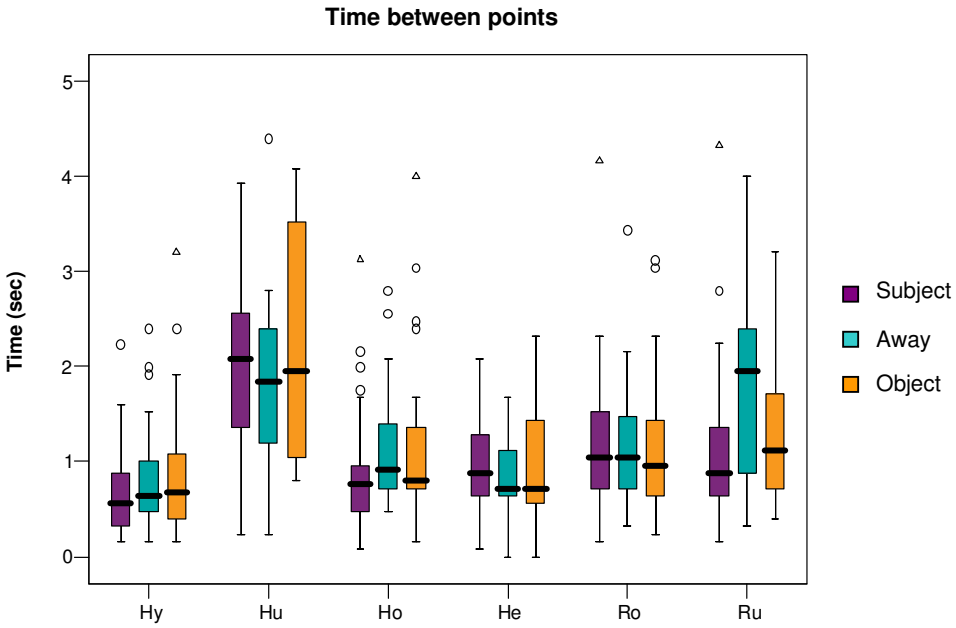

Figure 4.15 – Time between points. For each subject, the average amount of time between the end of one point and the beginning of the next point for all points in a trial. Bold lines represent the median length of time; the boundaries of each box represent the inter-quartile range. Whiskers represent the range, while outliers are marked by circles and triangles. No significant differences were found.

4.2.3 – Discussion

Although their use of pointing in Experiment 1, a context different to that in which they were trained, was surprising and impressive, lemurs had failed to modify their use of pointing when I was not attending to them. I reasoned that perhaps since they were using the gesture in a new context, there were many distracting factors for the animals that could have affected their performance and added "noise" to the data. I chose, then, to examine their pointing in a paradigm more similar to that in which they were trained to point in order to see whether differential pointing would occur under more familiar conditions. However, lemurs did not alter their gesture use based on my attentional state in this experiment either.

Many researchers have cited sensitivity to an observer's attentional state as a requirement for intentional communication (Woodruff & Premack, 1979; Bruner, 1981; Call & Tomasello, 1994; Tomasello et al., 1994; Leavens & Hopkins, 1999; Hostetter et al., 2001), as the signaller must understand that the gesture needs to be perceived by the observer in order to achieve the desired outcome. The results of Experiments 1 and 2 suggest that lemurs are unable to meet this requirement when using a trained pointing gesture to obtain food from a human observer. Lemurs gestured equally often whether I could see their gesture or not, rather than using the gesture more when I could perceive it. As such, they may not understand their trained gestures as communicative.

4.3 – General Discussion

In their study with chimpanzees, Russell and colleagues (1997) found that subjects not only alternated gaze between a novel toy and a human caregiver's face, but also did so in very long sequences. While all subjects engaged in gaze alternation bouts consisting of their minimum criterion of three looks, 65% of subjects exhibited bouts of more than three looks, with the observed maximum being eight looks. The lemurs in my experiments performed similarly in this regard. All subjects engaged in gaze alternation bouts consisting of three looks (despite my lower criterion of two looks), and all subjects exhibited bouts of more than three looks, with the observed maximum being a length of eleven looks. Squirrel monkeys have also been shown to engage in gaze alternation while pointing (Anderson et al., 2007), just as chimpanzees have (Tomasello et al., 1985; Leavens et al., 1996; Krause & Fouts, 1997; Russell et al., 1997; Leavens & Hopkins, 1998; Leavens et al., 2004). This led Anderson and colleagues (2007) to conclude that if pointing in monkeys is functionally different from pointing in apes, then it is not by way of gaze alternation. There must be other criteria, then, that make pointing in apes more 'special.'

Sensitivity to attentional state is one sign of intentional communication (Woodruff & Premack, 1979; Bruner, 1981; Tomasello et al., 1994; Leavens & Hopkins, 1999; Hostetter et al., 2001). Apes modify their use of gestures depending on the attentional state of the recipient in both natural (Tomasello et al., 1994; Liebal et al., 2004) and experimental (Call & Tomasello, 1994; Krause & Fouts, 1997; Hostetter et al., 2001; Kaminski et al., 2004; Poss et al., 2006; Bulloch et al., 2008) conditions, but monkeys do not (Hattori et al., 2007). In the experiments described in this chapter, I found that lemurs are also unable to modify their use of a trained

pointing gesture, despite their frequent looks to my face and thereby ample opportunity to recognise my attentional state. However, lemurs have been reported to fail to visually co-orient with humans (Itakura, 1996; Anderson & Mitchell, 1999), and this may suggest that they are unable to recognise human attentional states at all, never mind whether they possess the capacity to appropriately modify their use of visual signals according to these attentional states.

I did not present subjects with a front-back condition, and perhaps lemurs would modify their behaviour in response to a cue as gross as body orientation, as even non-primates are able to make this distinction (e.g. dolphins, Xitco et al., 2004). Even so, if lemurs were able to point differentially in response to body orientation, it would not imply that lemurs understand attention. Paradigms that require extensive training, as the lemurs were extensively trained to point, often result in cue discrimination rather than social understanding (Gómez, 1998). In such a case, lemurs' differential pointing in an experiment using body orientation cues might be a result of cue discrimination, as they were trained to use the pointing gesture under conditions in which an experimenter was facing forward. Alternatively, a differential response could reflect an understanding that body orientation correlates with a disposition to provide food rewards, as has been found in apes (Kaminski et al., 2004).

It is worth noting that the cost of pointing in my experiments is minimal. Lemurs did not lose anything by pointing more than once when their first or second gestures were ineffective, and they received their food after just five seconds. Perhaps the combined influence of the extensive training of the gesture, and the fact that lemurs incurred no cost for pointing under the "wrong" conditions, meant that lemurs had no need to recognise the "right" ones. In an experiment in which the delay were

60 seconds, or even more, the cost of staying with the experimenter would be greater, as subjects could use that time to eat lower-quality food available in the enclosure, or approach the door separating the inside (testing) and outside (waiting) areas in order to vocalise to group members (this is one of the lemurs' favourite activities). I speculate that under conditions of higher cost, lemurs might then use attentional cues to modify their behaviour. For example, lemurs might leave the experimenter more quickly when she is not attending than when she is.

Gaze alternation and attentional state sensitivity, however, are not the only behaviours that suggest intentional communication. Persistence of pointing until the goal is reached (Bruner, 1981; Leavens & Hopkins, 1999; Cartmill & Byrne, 2007) and using pointing for a referent other than that for which it was trained (Call & Tomasello, 1994), such as pointing deceptively in the presence of a competitor (Woodruff & Premack, 1979; Anderson et al., 2001) are other behaviours that researchers have suggested would imply an animal's behaviour is intentionally communicative. There is some evidence that these same lemurs can learn to point deceptively (black lemurs: Genty & Roeder, 2006; brown lemurs: Genty et al., 2008), but only one brown lemur (Hutch) learned to do so with any reliability.

Intentional communication requires that a signaller understands others not as mere agents (as defined as entities able to generate their own movements), but as subjects. Baron-Cohen (1991) has argued, however, that protoimperative pointing (defined as requestive pointing, or pointing to use another individual to obtain an object (see also: Bates et al., 1979; Leavens & Hopkins, 1998)) does not require the attribution of mental states, as it can be managed by the use of behavioural cues and physical interactions alone. Perhaps lemurs are behaviourists in the context of these experiments, and do not recognise nor reason about the mental states of others. In

other words, they aimed only to change my behaviour through using their gesture, but did not understand that I must see the gesture in order for it to be effective. Their frequent looks to my face, then, could have served as a way to check for some behavioural cue that would provide information about my future behaviour (Tomasello & Call, 1997), and indicate whether I was about to provide food or not. For example, they could have been searching for a threatening gesture, or could have been looking to see if I was eating the food myself. In either case, lemurs' use of gaze alternation might not differ depending on whether or not I could see them. Instead, alternating glances between the food reward and my face would be interpreted as focusing on the raisin and searching for information about whether they would obtain it. Checking to another individual's face in order to predict that individual's future behaviour is also part of social referencing (Phillips et al., 1992). And since this explanation does not involve an understanding that a gesture must be seen in order to be effective, lemurs' pointing might not differ depending on my attentional state either.

Recognising the attentional states of another individual and using this information to modify one's own behaviour is an ability that is valuable not only to gestural communication, but also to other aspects of social living such as locating resources in the environment through gaze-following. This is the topic of the next chapter.

Chapter 5*

In the previous chapter, I discussed the value of recognising self-directed gaze, that is, recognising that another individual is looking at you. However, recognising when another individual is looking somewhere other than oneself and following the direction of that individual's gaze, are also valuable skills (Anderson & Mitchell, 1999). Following the gaze of others offers many opportunities for a social animal: to locate food sources, to detect predators, and to witness important social interactions (Emery, 2000; Zuberbühler, 2008). It also provides information helpful in predicting another individual's behaviour (Seyama & Nagayama, 2005). For humans, visual co-orientation is recognised as a crucial component of language and social learning (Bruner, 1983; Csibra & Gergely, 2006) and is also thought to be important in development of theory of mind (see Chapter 6), including the ability to deceive intentionally (Whiten & Byrne, 1988) and to attribute intentions to others (Santos & Hauser, 1999).

While some researchers have speculated that lemurs might follow the gaze of conspecifics (Anderson & Mitchell, 1999), systematic evidence is very meagre for prosimian primates, just the species whose evolutionary history is key to understanding the phylogenetic pattern. In a recent study by Shepherd and Platt (2008) exploring visual orienting in ring-tailed lemurs, two male individuals were fitted with eye-tracking video cameras to be worn while engaging in everyday

* The results of Experiment 2 and the details of "gaze priming" (proposed in the General Discussion of this chapter) were recently published: Ruiz, A., Gómez, J.C., Roeder, J-J, & Byrne, R.W. (In press) Gaze following and gaze priming in lemurs. *Animal Cognition*. DOI: 10.1007/s10071-008-0202-z

interactions and movements. Their data suggest that ring-tailed lemurs may engage in some co-orientation, but this issue remains to be experimentally tested and systematically investigated. This is the aim of this chapter.

5.1 – Experiment 1: Do lemurs follow the gaze of conspecifics?

Researchers tracing the evolution of visual co-orientation among primates have typically asked whether subjects were able to follow the line of gaze of a human experimenter. In these studies, the experimenter would stand in front of the subject and direct his attention to a location in the testing room using cues such as head orientation and eye gaze direction. Great apes (Itakura, 1996; Povinelli & Eddy, 1996a; Tomasello et al., 1999; Tomasello et al., 2001; Brauer et al., 2005) and Old World monkeys (Anderson & Mitchell, 1999; Ferrari et al., 2000; Tomasello et al., 2001; Goossens et al., 2008) have been shown able to follow human gaze, whereas prosimian primates have failed at this task (Itakura, 1996; Anderson & Mitchell, 1999).

Visual co-orientation with a conspecific may be more biologically salient and, thereby, a more valid test (Neiworth et al., 2002). Fewer studies have investigated following a conspecific's gaze, but these have reported similar gaze-following abilities in a wider range of species. In a study with chimpanzees and four Old World monkey species, Tomasello and colleagues (1998) enticed one individual to look at an attractive piece of food and then measured the reaction of a second individual (the subject) who had been looking at that individual. They found that all five species they tested reliably followed the gaze of conspecifics. Cotton-top tamarins, a New World

monkey species, were also shown to follow the direction of attention of a group mate, but not of a familiar human experimenter (Neiworth et al., 2002). Burkart and Heschl (2007) found that another New World monkey, the common marmoset, also follows the gaze of conspecifics.

Studies using live conspecifics models, however, present some methodological problems. Firstly, it can be difficult to be sure that the observer has not simply noticed the object of the other individual's attention, independently of following the other individual's gaze. In their study, Tomasello and colleagues (1998) overcame this problem by designing a control condition in which food was presented to the subject when it was alone, but not all studies incorporate such controls. Further, it is difficult to train a conspecific to direct the attention of another individual, in order to carry out more controlled tests (Neiworth et al., 2002; Horton & Caldwell, 2006), which limits the types of questions an experimenter can investigate using live conspecific models.

One promising development in socio-cognitive research is the successful use of photographic stimuli. Tests exploring visual co-orientation using photographs instead of live models have shown that Old World monkeys (Lorincz et al., 1999; Scerif et al., 2004) and apes (Horton & Caldwell, 2006) can successfully follow the direction of a photographed conspecific's visual attention. In these studies, subjects are presented with a static image of a conspecific, either on video screen or paper. This paradigm allows the experimenter to strictly control what cues are made available to the subject, in what specific direction the model is 'attending', and how much time the subject is exposed to the cue. These factors make possible more detailed analyses and a wider range of experimental questions.

In addition, some non-primate species also show evidence of visual co-orientation. Domestic dogs are able to follow the attentional cues of both humans and

members of their own species (Hare & Tomasello, 1999; Ittyerah & Gaunet, In press), as are ravens (Bugnyar et al., 2004), while goats' skills are limited to following the gaze of conspecifics, and do not extend to humans (Kaminski et al., 2005). These results, given the apparent absence of gaze following in prosimians (Itakura, 1996; Anderson & Mitchell, 1999), raise the possibility that the cognitive skills allowing gaze following have evolved independently in different taxa. However, if instead gaze following were found in prosimians, then it would most likely be primitive in mammals, rather than derived independently in dogs, goats, and simians.

Before an individual can benefit from visual co-orientation, however, it must first recognise and utilise the correct cues to orientation. As the social environment of humans and other primates is a busy one, this may not be an easy task. Baron-Cohen (1994; 1995) proposed a mechanism called the eye-direction detector (EDD) that would achieve this task by detecting the presence of eyes in the environment and then determining the direction of visual attention using the position of the iris relative to the sclera. Baron-Cohen's emphasis on eyes, however, is problematic. Firstly, information from another individual's eyes may not always be available, as that individual may be too far away for the observer to see its eyes clearly, or its eyes may be occluded by shadow or other objects in the environment (Perrett et al., 1992; Emery, 2000). Secondly, although the eyes are a clear signal for humans due to the presence of a transparent conjunctiva and large white sclera, Kobayashi & Kohshima (1997) found, in their study of close to 100 species of primate, that this feature is unique in the primate order. As such, judgements about direction of visual attention based only on the eyes would be difficult for other species.

Neurophysiological evidence suggests that information from the eyes is not the only cue used by non-human primates. For example, there are neurons in the

macaque superior temporal sulcus that are sensitive to specific orientations of the body (Wachsmuth et al., 1994) and head (Perrett et al., 1991; Perrett et al., 1992). Further, there are individual cells that seem to respond to perceived direction of attention, e.g. looking downward. These neurons fire not only when subjects are presented with models whose eyes are pointed downward, but also when the model's head or body pointed downward, in the absence of other cues (Perrett et al., 1992; Perrett & Emery, 1994). While the vast array of cues available for use in determining another individual's direction of attention can be beneficial, because inferences can be made as long as at least one of these is available, problems could potentially arise when two or more of these cues present conflicting information (Seyama & Nagayama, 2005).

In light of this evidence, Perrett and Emery (1994) proposed a direction-of-attention detector (DAD), which credits eye gaze as well as head and body orientation as cues used in determining another individual's direction of attention. They suggest that this mechanism would work in such a way that information from different cues would be organised in a hierarchy. Information from the eyes would override information from the head, and information from the head would override information from the body, due to a network of inhibitory connections in cortex. As such, this system would not only allow for computation of attention direction when some cues are unavailable, but also when cues contradict one another.

In macaques, Lorincz and colleagues (1999) observed that subjects behaved in a way similar to that predicted by the DAD model. They presented monkeys with photographs of conspecifics directing their attention to a specific location. In one condition the model's body and head were oriented in different directions, and in another condition the model's head and eyes were oriented in different directions.

Subjects co-oriented with head rather than body direction in the first condition, and with eye rather than head direction in the second.

Although there is strong evidence that Old World monkeys correctly follow head orientation when cues from body orientation provide conflicting information (Lorincz et al., 1999), it remains to be seen whether this capacity is also found in primates more distantly-related to humans: the prosimians. The purpose of this experiment, then, was two-fold. I aimed to determine experimentally whether lemurs are able to visually co-orient with conspecifics. Within the same paradigm I also aimed to explore what cues lemurs would use to do so.

5.1.1 – Method

Subjects

Subjects were three brown lemurs (Hyacinthe, Hutch, and Hermine) at the Centre de Primatologie de l'Université Louis Pasteur, Strasbourg, France, and three red-fronted lemurs (Scortcha, Jack, and Roxanne) at the Blackpool Zoo in Blackpool, United Kingdom, as described in Chapter 2.

Procedure

The experimental stimuli were full-colour photographs of a conspecific familiar to the subject but not participating in the present study (hereafter: model), looking to the left or to the right. In the Agreement condition, the model's body and head were oriented toward the same direction (left or right). In the Disagreement

condition, the model's body and head were oriented toward opposite directions (see Figure 5.1 for examples). Non-test stimuli (photographs of familiar outdoor scenes) were also presented in one-third of trials to prevent habituation.

Centre de Primatologie:

I tested each lemur individually, administering daily sessions consisting of nine trials. I presented the stimuli to each subject from the side of the indoor enclosure. In order for a trial to begin, the subject had to be seated directly in front of and looking at the display apparatus (a simple platform upon which stimuli were stacked, facedown). I then lifted up the stimulus from the top of the pile and displayed

Figure 5.1 – Examples of test stimuli in the Agreement (head and body oriented in the same direction; top) and Disagreement (head and body oriented in different directions; bottom) conditions.

it to the subject. After five seconds, the trial ended, I placed the stimulus face down, and then removed that particular stimulus from the display apparatus.

I placed stimuli on the display apparatus before testing commenced in pseudo-random order (with no more than three consecutive trials of the same condition or in which the model was oriented in the same direction). As I remained behind the stimuli, I was blind to the stimulus being presented in any given trial and could thereby not unintentionally provide additional cues to the subject.

Blackpool Zoo:

Each trial was conducted opportunistically from the side of the lemurs' enclosure. In order for a trial to commence, the subject had to be near the viewing window and not engaged in any activity that would interrupt the trial or affect performance (e.g. foraging, grooming, eating). I drew the subject's attention to the display apparatus (an easel upon which stimuli were presented) using novel objects and vocal signals. When the subject was looking at the apparatus, I revealed the stimulus by flipping back a piece of paper that was covering the photograph. After five seconds, the trial ended, the cover was replaced, and that particular stimulus was removed from the apparatus.

Stimuli were stacked on the display apparatus at the beginning of the day in a pseudorandom order (with no more than three consecutive trials of the same condition, or in which the model was oriented in the same direction). As I remained behind the stimuli, I was blind to the stimulus being presented in any given trial and could thereby not unintentionally provide additional cues to the subject.

The length of test sessions ranged from one to five trials, due to subjects' varying willingness to participate and the presence of the wide array of distractions in a zoo environment.

Analysis

Only looks that occurred directly after looking at the model, and within the 5 second trial window, were included in analyses. I classified looks of an angle less than 90 degrees from the model's gaze as "target," and looks of an angle less than 90

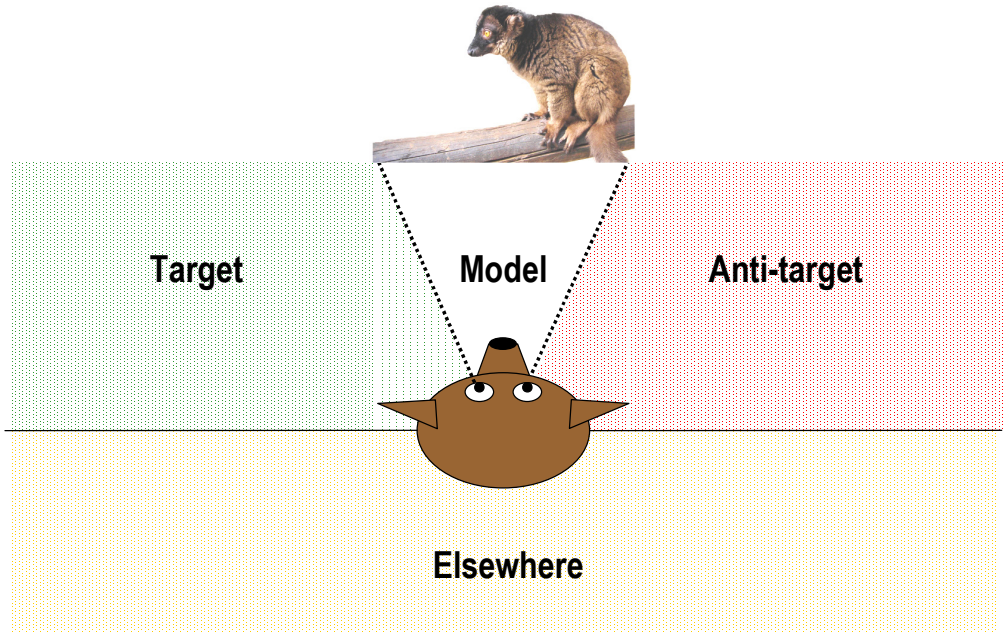

Figure 5.2 – Coding criteria. Upon seeing the model, I coded subjects' looks in the same direction as the model's gaze as "target" (green), and looks in the direction opposite to the model's gaze as "anti-target" (red). Looks of an angle greater than 90 degrees from the model were recorded as "elsewhere" (yellow). Only looks that occurred directly after seeing the model were recorded.

degrees from the direction opposite to the model's gaze as "anti-target" (Figure 5.2).

For each trial, I recorded the direction of the subject's first inspection (target or anti-target) upon seeing the model of at least 80ms duration (as in Scerif et al., 2004; Horton & Caldwell, 2006), and the time the subject spent looking in each of these directions. As video was filmed from behind the presentation, I was able to code each trial blindly.

Trials were removed from analysis if subjects' behaviour was affected by external stimuli, such as vocalisations from other animals and visitor distractions (e.g., subjects moved out of the testing area during the trial).

To assess inter-observer reliability, a second researcher not associated with the experiment coded 20% of trials. In determining the location of subjects' first visual inspection upon seeing the model, 89.5% agreement was achieved (Cohen's K=0.79, an "excellent" value (Bakeman & Gottman, 1986)). Pearson's correlation also revealed a high level of agreement for the total time subjects spent looking in the target and anti-target directions (r=0.69, $p<0.001$).

5.1.2 – Results

First visual inspection

To determine whether subjects co-oriented with the model, replicated goodness of fit tests (Sokal & Rohlf, 1995) for observed ratios of subjects' first visual inspections (target to anti-target direction, null hypothesis 1:1) were run in both the Agreement and Disagreement conditions. Tests for heterogeneity were insignificant in

both conditions (Agreement: G=6.00, df=5, *P*=0.31; Disagreement: G=1.38, df=5, *P*=0.93), indicating that the data were homogenous across subjects and thereby allowed analysis at the group level. The outcome of those analyses was significant in

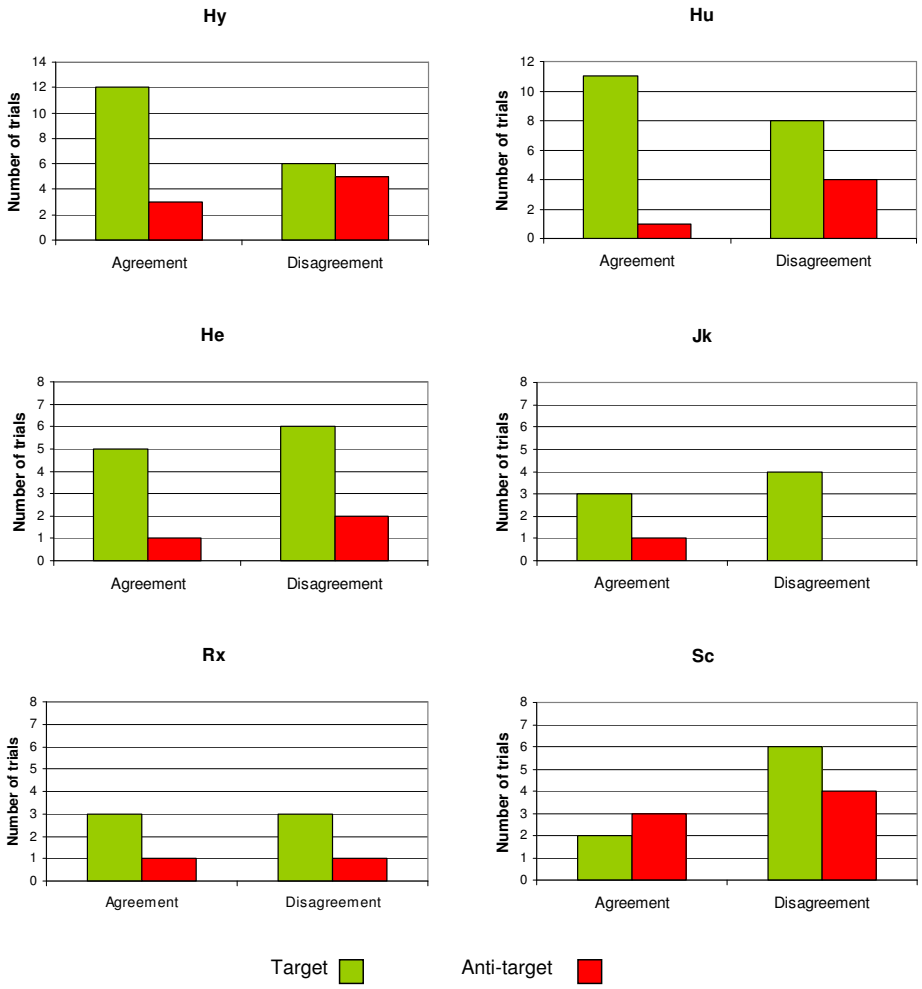

Figure 5.3 – Location of first visual inspection. The number of trials in which each subject looked to the target or anti-target locations directly after seeing the model for the first time for that trial.

both conditions (Agreement: G= 9.96, df=1, *P*=0.002; Disagreement: G= 8.83, df=1, *P*=0.003), showing that lemurs first looked in the target direction significantly more often than they first looked in the anti-target direction (Figure 5.3).

Looking time

To explore whether subjects also spent more time looking in the same direction as the model, I compared the average time subjects spent looking in the target and anti-target directions for the duration of the trial (Figure 5.4). One-way

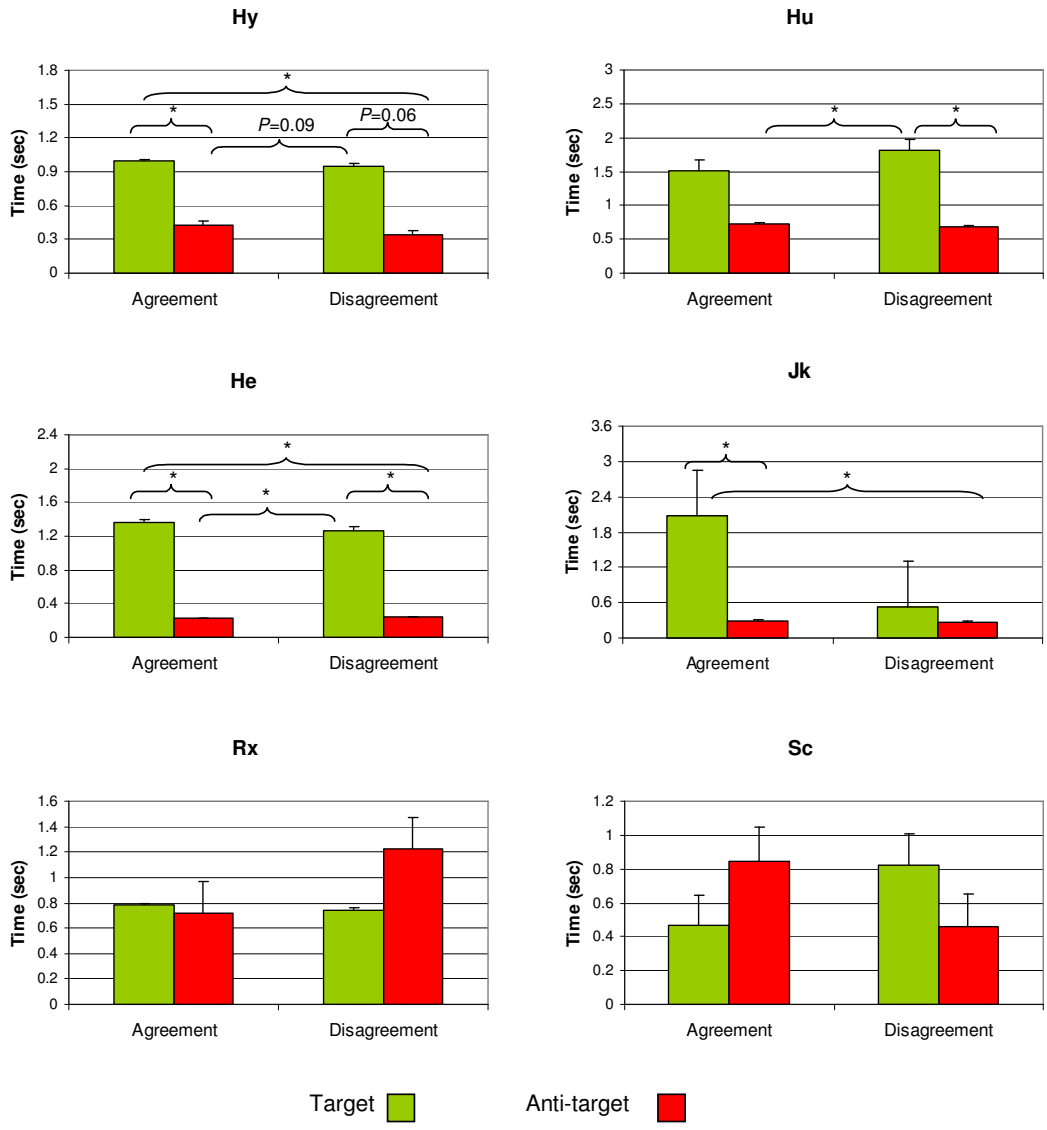

Figure 5.4 – Average looking time per trial. The average time per trial each subject spent looking in the target and anti-target directions directly after seeing the model. Tukey post-hoc tests : * $P \leq 0.05$

ANOVA tests were conducted for each subject and revealed significant differences in looking time for four out of six subjects (Hy: F=4.87, df=3, *P*=0.005; Hu: F=3.90, df=3, *P*=0.015; He: F=5.52, df=3, *P*=0.005; Jk: F=4.08, df=3, *P*=0.03; Rx: F=0.252, df=3, *P*=0.89; Sc: F=0.810, df=3, *P*=0.50).

Tukey post hoc comparisons were conducted for those subjects whose ANOVAs yielded significant results (Hy, Hu, He, and Jk). Three out of four subjects looked significantly longer in the target direction than in the anti-target direction in the Agreement condition (Hy: *P*=0.04; Hu: *P*=0.23; He: *P*=0.045; Jk: *P*=0.05), and two out of four subjects did so in the Disagreement condition, with one more subject approaching significance (Hy: *P*=0.06; Hu: *P*=0.04; He: *P*=0.03; Jk: *P*=0.98). These looking time differences also held in cross-condition analyses. Three out of four subjects looked significantly longer in the target direction in the Agreement condition than they looked in the anti-target direction in the Disagreement condition (Hy: *P*=0.02; Hu: *P*=0.19; He: *P*=0.03; Jk: *P*=0.05). Two out of four subjects looked significantly longer in the target direction in the Disagreement condition than they looked in the anti-target direction in the Agreement condition, with one more subject approaching significance (Hy: *P*=0.09; Hu: *P*=0.05; He: *P*=0.05; Jk: *P*=0.98).

Post hoc analyses also revealed that none of these four subjects looked significantly longer in the target direction in the Agreement or in the Disagreement conditions when they are compared to each other (Hy: *P*=1.0; Hu: *P*=0.89; He: *P*=1.0; Jk: *P*=0.10). Further, they did not look significantly longer in the anti-target direction in one condition than the other (Hy: *P*=0.98; Hu: *P*=1.0; He: *P*=1.0; Jk: *P*=1.0), indicating that neither condition was more or less effective than the other in eliciting a co-orientation response.

5.1.3 – Discussion

This study provides experimental evidence that two species of prosimian primate are able to follow the gaze of conspecifics. This contrasts with earlier negative findings with human models (Itakura, 1996; Anderson & Mitchell, 1999), thereby supporting the idea that more ecologically valid methods need to be used when possible in order to understand fully the abilities of non-human species (Hare, 2001). This interpretation is further corroborated by the instances of co-orientation reported by Shepherd and Platt (2008) in free-ranging lemurs.

Because some non-primate mammals show evidence of gaze following (Hare & Tomasello, 1999; Kaminski et al., 2005), evidence of the presence or absence of this skill in prosimian primates was needed to indicate whether this ability evolved independently in different mammalian taxa, or once in a single common ancestor. Prosimian data thus hold the key to the possibility that positive results in non-primate mammals (Hare & Tomasello, 1999; Kaminski et al., 2005) are due to ancient adaptation instead of convergent evolution. The results of Experiment 1 provide experimental evidence that prosimians are indeed able to follow conspecific gaze as expressed through the orientation of head and eyes jointly, implying that this cognitive skill is, at the very least, primitive for all primates. I suggest, therefore, that gaze following might have evolved only once among mammals. The abilities of birds such as ravens (Bugnyar et al., 2004), however, may reflect independent evolution of the same skill, though further exploration into the abilities of non-mammal species is needed.

Like Old World monkeys (Lorincz et al., 1999; Scerif et al., 2004) and apes (Horton & Caldwell, 2006), lemurs are able to co-orient with a static image of a

conspecific. This indicates that properties of the face are sufficient to elicit a gaze-following response, without the presence of other cues, such as motion or vocalisations.

In addition, these results show that, like macaques (Lorincz et al., 1999), lemurs are able to co-orient effectively when the visual cues available to them provide contradictory information. When following another individual's direction of attention, lemurs were able correctly to use information provided by the orientation of the head, despite potentially contradictory information provided by the orientation of the body. Shepherd & Platt (2008) had suggested that this might be the case, based on observations of two free-ranging ring-tailed lemurs. My experiment provides controlled experimental evidence for this ability.

Some researchers have proposed that conflicting information might be a more salient cue to direction of attention than non-conflicting information. An incongruity of head and body orientation, for example, could imply that something has alerted that individual and caused it to rotate its head, whereas having one's body, head, and eyes aligned is often a resting position (Jellema & Perrett, 2003). The idea of salience of implied motion has support from neurophysiological data that shows certain cells in macaque superior temporal sulcus fire upon seeing a static image that implies motion (Jellema & Perrett, 2003), an effect that was also found in human subjects (Kourtzi & Kanwisher, 2000). More specifically, while a normal congruity effect has been shown in human subjects for the direction of head and eyes (Langton, 2000; Seyama & Nagayama, 2005), a reverse congruity effect has been shown for eye and body direction (Hietanen, 1999; Hietanen, 2002; Seyama & Nagayama, 2005), as well as head and body direction (Hietanen, 1999; Hietanen, 2002). That is, judgement of gaze direction was faster in human subjects when the eye and head cues of a model were in

agreement than in disagreement, but slower when eye or head cues were in agreement with body cues than when these were in disagreement.

I found that the photographic stimuli in Experiment 1 were equally effective in eliciting visual co-orientation in lemurs, whether the conspecific model's body and head were oriented in the same or opposite directions. That is, lemurs did not look more reliably, or spend more time looking in the target direction, in one condition rather than the other. So, despite the potentially confusing contradiction of cues in the condition where head and body were oriented in opposite directions or, alternatively, the potentially provocative nature of the conflicting cues, lemurs co-oriented with the model's direction of attention just as effectively as they did when all cues were providing the same information. However, as reaction time was not one of the measures I examined in this experiment, I cannot directly compare these results to those reporting congruity effects in humans. Videos of each trial could be analysed for latency to co-orientation, but this would still fall short of the reaction time accuracy of the human data.

The two subjects with no significant looking time effect in either condition, Roxanne and Scortcha, were both individuals at the Blackpool Zoo. As the nature of the study at this site involved conducting trials opportunistically, and given the high number of trials aborted due to the distractions associated with an uncontrolled zoo environment, these subjects received fewer trials than their Centre de Primatologie counterparts. This may have prevented any clear pattern in behaviour to emerge. It is worth noting, however, that the third individual at Blackpool zoo, Jack, did exhibit significant differences in some of the comparisons even though he completed as few trials as his group mates.

It has been suggested that, as their visual acuity is not as high as that of simians, lemurs will be more likely to follow head orientation rather than eye gaze, as a primary signal of attention direction (Kay & Kirk, 2000). Further, there is evidence from work with other primates that cues from the eyes might not be given as great importance, as in humans. While there exist few studies that report non-human primates as able to spontaneously follow eye gaze direction (e.g. Lorincz et al., 1999), there are many that report the opposite. Capuchin monkeys have been shown to use head orientation instead of eye gaze direction when the two provide conflicting information (Vick & Anderson, 2000). Apes have been shown to follow head direction even when eyes are closed, though they did so more often when eyes were open, whereas human children were shown to rely more on eye gaze direction in the same paradigm (Tomasello et al., 2007). Human infants were also found to follow an adult's direction of attention more often when eyes were open and not occluded (Brooks & Meltzoff, 2002).

To explain these findings, Tomasello and colleagues (2007) proposed the "cooperative-eye hypothesis." They suggest that human-type eyes evolved in the context of pressures for enhanced communicative and cooperative abilities useful in mutualistic social interactions, such as joint attentional interactions. These types of interactions are collaborative activities around objects (Bard & Vauclair, 1984; Tomasello & Carpenter, 2005), which require participants to monitor to what others are attending, including whether attention is being paid to their own actions, so as to coordinate more effectively (Tomasello et al., 2005).

However, relying on head orientation, rather than eye direction, might not put an individual in a completely disadvantageous position. It has been argued that the two cues are virtually equal as reliable indicators of another individual's attention as

they are most often congruent (Corkum & Moore, 1995), especially since primate eyes are forward-facing (Moore & Corkum, 1994). Further, if eye direction information were not always easy to obtain, as in non-human primates, focusing on features that are easier to detect (e.g., head orientation) would be more efficient (Kaminski et al., 2004).

The results of the current experiment show that lemurs rely on head orientation when presented with conflicting information from the body. While these data begin to support the direction-of-attention detector (DAD) model proposed by Perrett and Emery (1994), further work will be needed to explore whether lemurs are able to follow conspecific eye gaze, and also whether they are able to use body orientation in the absence of other cues.

5.2 – Experiment 2: Do lemurs use conspecific gaze to locate food items?

Despite all the evidence that non-human primates have visual co-orientation skills, individuals of the same species are often reported to be unable to use the information provided by others' gaze for any practical purpose, such as locating a hidden object. The task generally used to assess use of gaze is the object-choice paradigm. In object-choice tasks, subjects must follow visual cues provided by an experimenter to choose one of two (or more) potential hiding places in which a food item has been placed. Evidence that any non-human primate possesses this ability has been inconsistent. Even though orangutans and gorillas follow human gaze (Itakura, 1996; Brauer et al., 2005), they appear unable spontaneously to use the cues provided

in object-choice tasks, although some improvement with extensive training has been reported (Peignot & Anderson, 1999; Byrnit, 2004; Byrnit, In press).

Chimpanzees have also been shown to co-orient with humans (Itakura, 1996; Povinelli & Eddy, 1996a; Tomasello et al., 1999; Tomasello et al., 2001; Brauer et al., 2005), yet subjects typically fail to reliably select the correct location in the traditional task (Call et al., 2000; Hare & Tomasello, 2004), and only perform successfully under certain limited circumstances. These include having the experimenter approach and search the correct location before allowing the subject to choose (Itakura et al., 1999; Buttelmann et al., 2008) or presenting the task in a competitive context in which an "evil" experimenter, who always takes food from the subject, uses reaching as a cue to the correct location (Hare & Tomasello, 2004). While the success of these experiments provides important insight into the types of ways in which researchers should frame experimental questions, these do not provide evidence that subjects are routinely able to use visual attention to discover hidden resources.

A study by Barth and colleagues (2005) revealed that chimpanzees were better at using visual attention when they were required to leave the testing area between trials, rather than remain for multi-trial blocks. Other researchers have found that accompanying gaze with vocalisations also seems to help chimpanzees choose correctly more often (Itakura et al., 1999; Call et al., 2000). Call and colleagues (1998) reasoned that the traditional object choice task is potentially confusing as the human providing the cues is looking at an inherently uninteresting overturned cup. They speculated that if the experimenter had visual access to the food item, while the chimpanzee did not, its performance might be enhanced. Their data support exactly that, as the chimpanzees chose correctly more often when food was hidden inside tubes or behind barriers, rather than underneath cups.

A recent study by Hauser and colleagues (2007) reported that rhesus macaques could use a conspecific-like communicative head gesture or a pointing gesture, both provided by a human experimenter, when choosing to search for a food reward in one of two boxes. However, this paper also reported that rhesus failed to use human head orientation and eye gaze cues to solve the task, even though this species has been shown to follow human gaze cues in previous studies (Anderson & Mitchell, 1999; Ferrari et al., 2000; Tomasello et al., 2001). Possession of a valuable cognitive skill without the ability to use it for such an adaptive purpose as finding hidden food resources presents an evolutionary paradox, calling into question the functional (Schloegl et al., 2008) and adaptive (Gómez, 2005b) value of gaze following skills. One possible resolution of this paradox might be that gaze following has evolved for some other function than foraging and, in non-human primates, it remains dissociated from foraging capabilities.

Some of these results, on the other hand, could reflect motivational rather than cognitive deficits (Tomasello et al., 1998). Simply, primates may be most interested in what other individuals of their own species are looking at and, as a result, might not reliably interpret human gaze as conveying information even when they automatically follow human gaze. The ability to recognise the informational content of human gaze might involve a re-routing of cognitive resources already in existence for conspecific communicative skills, in order to read human cues (Tschudin et al., 2001), or might require extensive contact with humans in order to enhance possible predispositions to attend to human cues (Scheumann & Call, 2004). In fact, the non-human primate subjects who tend to perform best on these tasks are those individuals that are highly enculturated (Itakura, 1996; Itakura & Tanaka, 1998; Agnetta et al., 2000; Call et al., 2000; Vick et al., 2001), lending support to the latter proposal. Further, various

studies have shown that aquarium dolphins (Tschudin et al., 2001) and fur seals (Scheumann & Call, 2004), who spend their days with human trainers, and also domesticated dogs (Hare et al., 2002) are able to use human gaze cues in object choice tasks.

Still, primates' difficulty in solving the object-choice task may not mean they are incapable of applying a strategy involving gaze following at all, just that it does not appear spontaneously in the conditions of these types of paradigm (Anderson et al., 1996). The object-choice task is a tricky one in that the subject must figure out that the gaze cue being presented by the experimenter is relevant to the food search task with which it is confronted in the first place when, if seen as a problem-solving task, anything in the environment could be a clue (Call et al., 2000). It follows, then, that a good way to look at subjects' performance in the object choice task is to also analyse how often they use gaze cues in the same study, and compare these data to choice performance in a trial-by-trial analysis. However, researchers using the object-choice paradigm have not investigated subjects' gaze-following responses along with subjects' choices in each trial.

I therefore modified the traditional object-choice paradigm in order to study both gaze following and object choice within the same experiment. I predicted that by analysing these two measures in tandem I would be able to determine whether co-orientation has any direct bearing on the evolution of attention understanding. If lemurs are able to co-orient but fail to incorporate this information in choosing a search location, this could suggest that gaze following evolved for another function altogether. A correlation between co-orientation and choice, however, would be testament to the evolutionarily adaptive value of gaze following, as a simple way of reading the attentional focus of others.

5.2.1 - Method

Subjects

Subjects were four brown lemurs (Hyacinthe, Hutch, Honorine, and Hermine) and two black lemurs (Rousse and Rustine), as described in Chapter 1.

Training

To accustom subjects to the experimental apparatus, I first gave subjects training sessions in which the location of the raisin was revealed before the subject made its choice. I presented each subject with a pivoting platform (70 X 16 X 25 cm), with a small opaque barrier on either end (15 X 8 cm), just as subjects would later experience in the test procedure. I placed both my hands behind the barriers, one behind each, while maintaining a neutral expression and looking straight ahead, and surreptitiously deposited a raisin behind only one. During these training sessions I lifted the barriers to reveal the raisin's location and then replaced them. The subject was then allowed to indicate one barrier to be removed by extending its arm toward one or the other barrier. I lifted the chosen barrier and rotated toward the subject its chosen side of the platform, allowing the subject to retrieve the raisin or to see that no raisin was available. In order to train subjects to attend to the full presentation, a trial was aborted and no reward was given if subjects reached before presentation was complete.

Training sessions consisted of ten trials, and each subject was permitted to complete one session per day. The location in which the raisin was hidden was pseudo-randomized so that five trials in a session were to the right, and five were to the left, with the raisin hidden in the same location in no more than three consecutive trials. Aborted trials were given again at the end of the session in order to maintain this balance. When a subject performed at 80% correct for two consecutive sessions, it was switched to the test procedure for subsequent trials.

Testing

The test procedure was similar to the training phase, except that I did not first lift the barriers to reveal the correct choice. Instead, I placed a full-color photo (15 X 15 cm) of the adult male of the group, with head and eyes oriented to the right or to the left, in the centre of the platform (Figure 5.5). The apparent gaze of this photographic model was always oriented to the barrier behind which I had placed a raisin at the start of the trial. The subject was then permitted to indicate one or other barrier. I lifted the selected barrier, revealing a raisin if the subject had chosen correctly or no raisin if the subject had chosen incorrectly. In either case, the indicated side of the platform was rotated toward the subject, allowing retrieval of the reward or showing the subject that no reward was available. I then reoriented the platform to its starting position and removed the model. The next trial began after the subject had consumed its reward (if it had chosen correctly), and only when the subject was sitting attentively in front of the apparatus, equidistant from each end.

As in the training phase, a trial was aborted and no reward was given if the subject did not attend to the full presentation before reaching. Also, trials in which

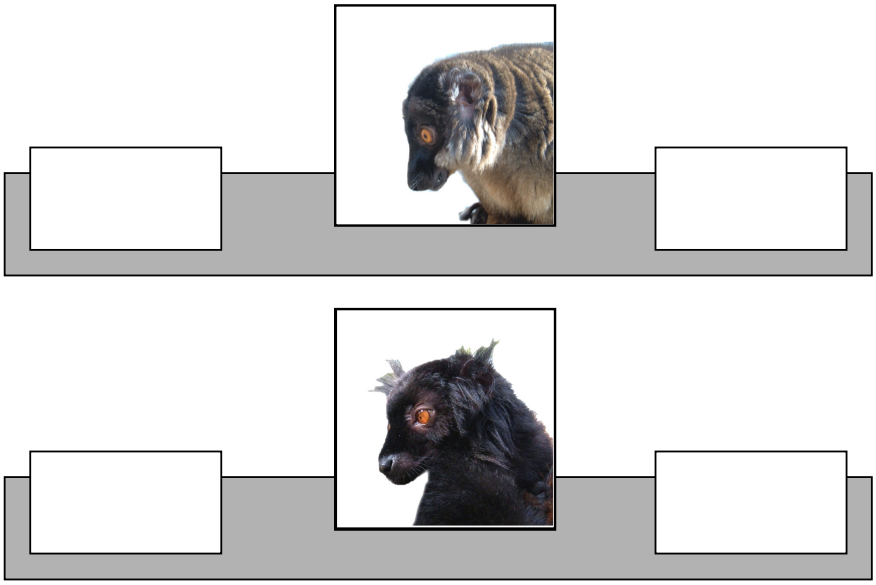

Figure 5.5 – Apparatus and experimental stimuli. A representation of the apparatus and stimuli presented to brown (top) and black (bottom) lemur subjects. An opaque barrier was sited on either end of a pivoting platform. After surreptitiously depositing a raisin behind only one, I placed in the centre of the platform a photograph of a known conspecific whose head and eyes were oriented towards the baited barrier.

subjects were distracted by outside stimuli (e.g., the vocalizations of other animals) were aborted during testing and given again at the end of the session.

Test sessions consisted of ten trials, and each subject was permitted to complete one session per day. As some individuals were more willing to participate than others, the number of trials completed for each individual differs, with the number of sessions per individual ranging from 14 to 21.

The direction in which the model was looking in a given trial was pseudo-randomized so that five trials in a session were to the right, and five were to the left,

with no more than three consecutive trials cueing the same direction. Before each session, a sliced raisin was rubbed on either side of the platform to ensure that lemurs could not use olfactory cues to locate the food reward.

Analysis

For each trial, I recorded the direction of the subject's first inspection upon seeing the model of at least 80ms duration (as in Scerif et al., 2004; Horton & Caldwell, 2006), and the subject's subsequent choice of barrier.

To assess inter-observer reliability, a researcher unassociated with the project coded 5% of trials. In judging the lemurs' choices, the secondary coder and I agreed on 100% of these trials (Cohen's K = 1). In judging the location of the subject's first visual inspection, we agreed on 94.6% of trials (Cohen's K = 0.89, an "excellent" value (Bakeman & Gottman, 1986)).

5.2.2 – Results

Visual co-orientation

Videos of each trial were coded for the location of subjects' first visual inspection. If lemurs are able to follow gaze, they should look towards the same location as the model. As in Experiment 1, I found that this was the case. Upon seeing the model, all subjects were significantly more likely to look at the barrier on the side to which the model was attending than to look at the other barrier (Binomial

probability, one-tailed: Hy, Hu, Ho: $P<0.001$, He: $P=0.043$, Ro: $P=0.016$, Ru: $P=0.002$; Figure 5.6).

Object-choice

Because the lemurs did not always follow gaze, and because they did not always act upon the first target their gaze fell upon, their overall pattern of choices superficially appeared to be random. Indeed, if analyzed simply for each individual's performance in object-choice, the data would resemble those chance performances reported by other object-choice experiments, with the lemurs' success ranging anywhere from 10% to 100% in a given session, and each subject's overall performance at chance levels (mean 53.8%, SD ± 16.8%). However, overall performance was not below 50% for any subject (Figure 5.7). In other words, although subjects did not appear to solve the task, all six seemed to be choosing correctly slightly more often than chance. As such, I continued analysis by using a replicated goodness of fit test (Sokal & Rohlf, 1995) for observed ratios of correct to incorrect choices (null hypothesis 1:1). A test for heterogeneity showed that the data were homogeneous (G=1.39, df=5, $P=0.93$), allowing me to conduct analysis on the pooled data. The outcome of this test was significant (G=6.78, df=1, $P=0.009$), meaning that, even though no subject did so individually, as a group subjects chose the correct search location more often than they did the incorrect search location.

To assess whether lemurs were learning over the course of the study, I examined each subject's performance using trend analyses (Sheskin, 2004). Five subjects did not show any significant upward trend across sessions (Hy: $t=0.48$,

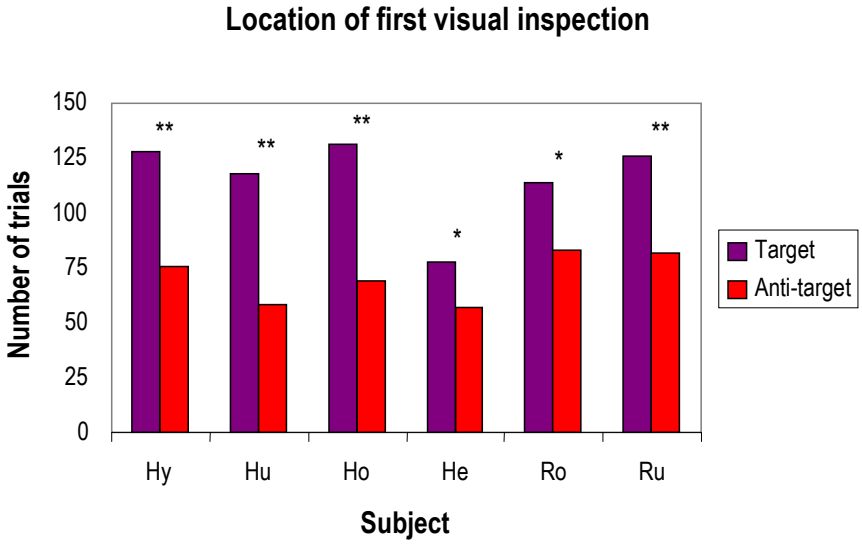

Figure 5.6 – Location of first visual inspection. Trials in which the subject first looked to the same location as the model ("target") and trials in which the subject first looked to the location opposite to that of the model's gaze ("anti-target"). Binomial probability: * $P<0.05$, ** $P<0.01$

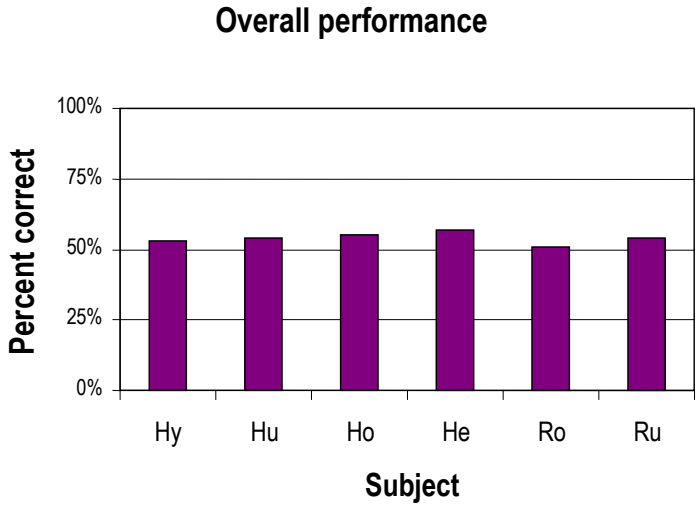

Figure 5.7 – Overall choice performance. Percent of trials in which each subject chose the correct search location (the barrier to which the photographic model was attending).

df=21, *P*=0.64; Hu: *t*=0.37, df=17, *P*=0.72; He: *t*=1.79, df=13, *P*=0.10; Ro: *t*=1.52, df=20, *P*=0.15; Ru: *t*=0.93, df=20, *P*=0.36), while one subject's performance did improve (Ho: *t*=2.86, df=20, *P*=0.01). This raised the possibility that Honorine's performance might be the cause of the finding that, as a group, subjects were able to choose the correct target more often than chance. I therefore repeated the replicated goodness of fit test (Sokal and Rohlf, 1995) for observed ratios of correct to incorrect choices (null hypothesis 1:1), excluding Ho from this analysis. A test for heterogeneity showed that the data were homogeneous (G=1.34, df=5, *P*=0.85), allowing us to conduct our analysis on the pooled data. The outcome of this test was significant (G=5.20, df=1, *P*=0.02), implying that, although Honorine's performance improved over the course of the experiment, this trend was not driving the effect.

When examining choice behaviour together with gaze following for each subject, I found that a subject's visual co-orientation and its ultimate choice of search location were closely linked. Using a chi-square test, I found that when a lemur successfully co-oriented with the model, it was significantly more likely to choose the correct location. When, instead, it looked to the location opposite to the model's gaze, it was more likely to choose the incorrect location (Hy: X^2=96.23, df=1, *P*<0.001; Hu: X^2=25.77, df=1, *P*<0.001 ; Ho: X^2=100.77, df=1, *P*<0.001; He: X^2=83.71, df=1, *P*<0.001; Ro: X^2=40.82, df=1, *P*<0.001; Ru: X^2=39.13, df=1, *P*<0.001; Figure 5.8). I also explored the connection between visual co-orientation and ultimate choice by conducting Pearson's correlations, which yielded similar results (Hy: *r*=0.69, df=1, *P*<0.001; Hu: *r*=0.38, df=1, *P*<0.001; Ho: *r*=0.71, df=1, *P*<0.001; He: *r*=0.79, df=1, *P*<0.001; Ro: *r*=0.46, df=1, *P*<0.001; Ru: *r*=0.43, df=1, *P*<0.001).

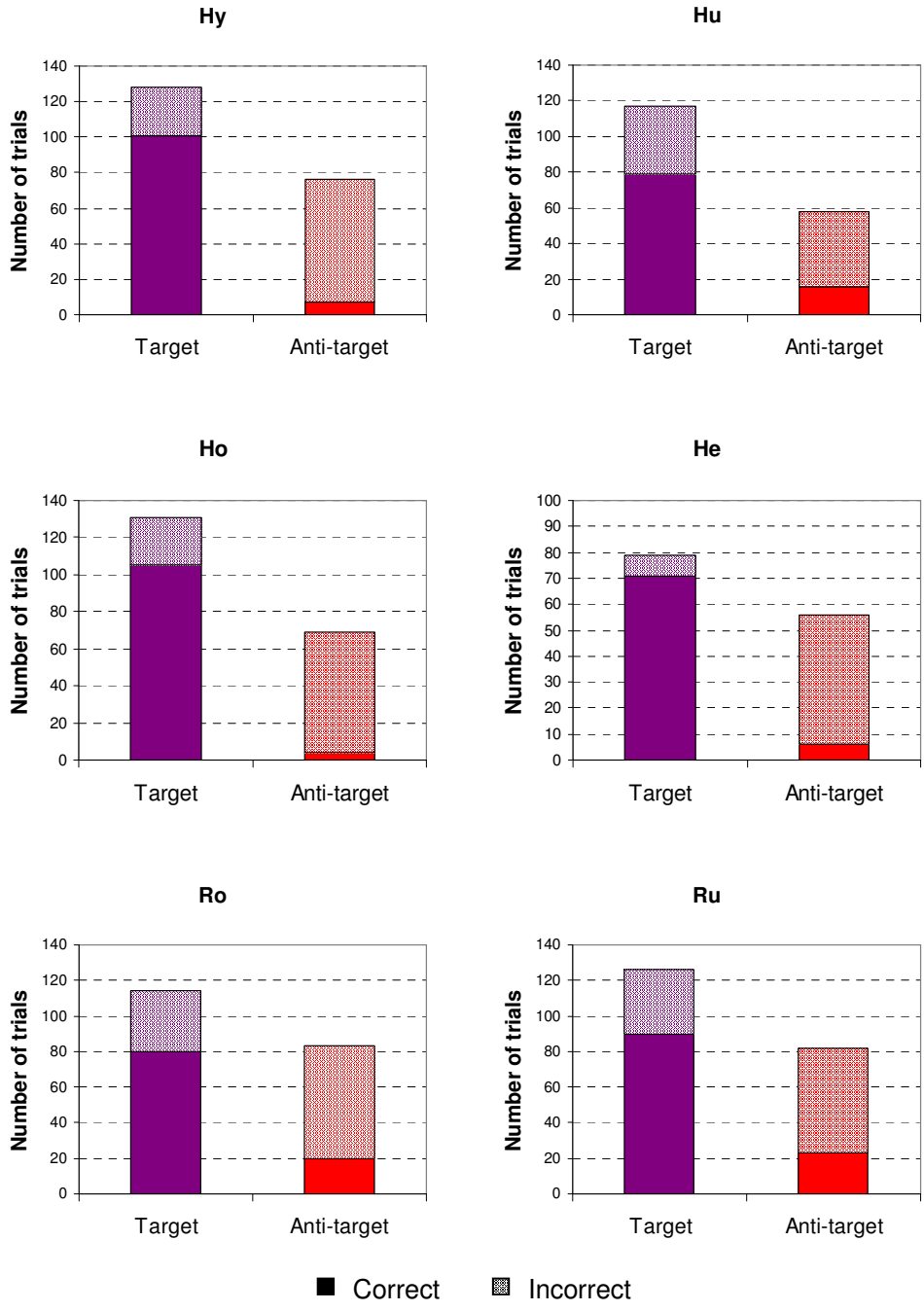

Figure 5.8 – First visual inspection and ultimate choice. Data showing both the location of first visual inspections and ultimate choice of barrier, grouped by subject. Trials in which the subject first looked to the same location as the model ("target") are in purple, and trials in which the subject first looked to the location opposite to that of the model's gaze ("anti-target") are in red. These data are further divided into correct (solid) and incorrect (patterned) choices.

So, when paired with the information provided by the lemurs' first visual inspections upon seeing the model, my analysis shows that when they follow gaze, lemurs do preferentially act upon the co-oriented target.

5.2.3 – Discussion

As in Experiment 1, the data concerning first visual inspection upon seeing the model provides further experimental evidence that lemurs are able to follow gaze of conspecifics.

Up to now, the abilities of non-human primates to interpret gaze have seemed puzzling: many species have been shown to look in the same direction as others, yet in object-choice tasks they failed to use this information to access hidden resources. This contrast presented a paradox: what is the function of gaze following if it is not used for such a basic function as locating resources? Clear conclusions have been hindered because object-choice tasks and studies exploring visual co-orientation, though investigating different aspects of the same ability, have remained separate. Although chimpanzees were shown to follow an experimenter's gaze in a sampling of trials in one object-choice experiment (Povinelli et al., 1999), neither this nor other studies have systematically explored visual co-orientation behaviour *in tandem* with subjects' responses. My results show that, when both factors are analysed together on a trial-by-trial basis, there is indeed a connection between visual co-orientation and foraging choices. While the mean object-choice performance of subjects hovered at chance levels, much like that of other species tested in similar experiments, this is because neither gaze following nor object choice work like a reflex. Lemurs did not always follow gaze, and they did not always choose the object at which they were

looking. However, if their gaze following and object choice were independent, one would expect a random distribution of choices whether or not the subject had followed the gaze of the model. What I find is precisely the opposite: that the lemurs' response to the model's gaze closely influenced their choice behaviour. When they followed gaze, they tended to choose the primed object; if they did not follow gaze, they tended to choose the non-cued object.

This link between gaze-following and ultimate choice is one that would have gone unnoticed without analysing together gaze following and choice. I therefore argue that other non-human primate subjects' failure to perform at a high level of correct choices in an object-choice task does not imply they are incapable of using gaze at all. I encourage other researchers to re-examine the details of their subjects' behaviour during these tasks in order to explore fully the link between gaze-following behaviour and the ultimate choice.

5.3 – General Discussion

While these results resolve the apparent evolutionary paradox, at least for lemurs, they do not necessarily indicate that lemurs are capable of full mentalistic attribution of perceptual states. In other words, the link between the lemurs' successful visual co-orientation and their above chance choice behaviour is not evidence that they understand gaze at the level of mental perspective taking – representing others as having the inner experience of seeing or attending. In such a case, sometimes called "high-level" gaze following (Tomasello et al., 1999; Burkart & Heschl, 2006), an individual follows the gaze of another in order to see what he is

seeing. In contrast to this stands “low-level” (Call et al., 1998; Burkart & Heschl, 2006) or ‘ecological’ (Butterworth, 1995) gaze following, in which an individual has a tendency to look in the same direction of others until seeing something of interest. The results presented in this chapter suggest something in between. Instead, it is possible that lemurs interpret gaze functionally without understanding the mental states involved, by tending to act upon objects at which they happen to be looking, and reliably looking at objects to which other individuals are attending – a phenomenon I call ‘gaze priming.’ Gaze priming is defined as the process by which an object or location becomes more salient for an observer, as a result of its following another individual's attention to that object or location. Depending on the social and environmental context, and the information gathered as a result of following gaze, this individual acts differentially in relation to that object. Consequently, the resulting behavioural response is flexible and can be appropriately different for dangerous or positive stimuli. On this hypothesis, visual co-orientation is indeed used to locate objects of interest in the environment (Emery, 2000; Zuberbühler, 2008) and could also be efficient as a mechanism of social learning, as has been postulated (Emery et al., 1997), but need not involve reasoning about unobservable mental states (see Chapter 6). What I report here is a candidate system for the evolutionary origins of more complex gaze following, as found in humans.

Chapter 6

It has been argued that social interactions monitored by the visual domain (e.g., individual recognition by sight rather than smell, recognising threatening or receptive body postures, witnessing which individuals engage in grooming or altercations with others) have played an important part in primate evolution, and that cognitive abilities (both social and non-social) have evolved along with social sophistication in primate species (Jolly, 1966; Barton, 1998; Emery, 2000). Some have claimed that although lemurs live in complex social groups, their performance on cognitive tasks fails to compare to that of simian species (e.g., Jolly, 1966). This has led to the idea that cognitive abilities emerged as a result of the demands associated with social complexity, and not vice versa (Jolly, 1966).

Since prosimian visual acuity is lower than that of other primates, researchers have suggested they rely on olfaction rather than vision (Brothers, 1990; Sauther et al., 1999; Kay & Kirk, 2000; Gilad et al., 2004). If prosimians do not navigate their social environment using visual attention, and are confirmed to not perform as well as simian primates on cognitive tasks, this would provide valuable evidence to support the hypothesis that visual social interactions created the necessary conditions for the evolution of complex cognition. In this case, prosimians' hypothesised reliance on olfactory or auditory information might explain the cognitive differences that have been reported for simian and prosimian primates.

Unfortunately, lemurs have until very recently often been left out of cognitive studies and have not been given a fair chance to prove their abilities, leaving a significant taxonomic gap in our understanding of primate cognition, as was pointed

out by Tomasello and Call (1997). Now a range of experiments have tested lemurs' abilities to manipulate tools, enumerate objects, and reason about ordinal relationships, and have shown that lemurs do have skills in object cognition that are very similar to those of monkeys, even though these tasks were given in the visual domain (e.g. Genty et al., 2004; Santos et al., 2005a; Santos et al., 2005b). It follows, then, that lemurs should be next tested in social cognition tasks in order to evaluate properly their social skills and determine whether these species are, after all, able to use social visual information.

The aim of my PhD was to systematically explore, for the first time, the socio-cognitive abilities of lemurs in order to begin filling this gap. I chose to focus on skills associated with social referencing: that is, the ability to gather and use appropriately social information (Feinman, 1982). As such, I aimed to find out whether lemurs attend to others in some contexts more than other contexts and in what ways any such changes in attention are manifest. I went on to explore whether lemurs are able to modify their behaviour based on the information they gather.

In this closing chapter, I will first summarise the findings of the six experiments that make up my dissertation. Next, I will consider what insight my results are able to provide into the cognitive systems that may be at play and how these results speak to whether lemurs are capable of mental state attribution. I will then discuss how individual differences in task performance might affect the interpretation of results, as well as how data collected from experiments with captive animals can relate to the behaviour of wild populations.

6.1 – Summary of findings

Here I will review the results obtained in the six experiments detailed in my dissertation by discussing several broad themes: in what contexts lemurs seek out social cues, to which social cues lemurs attend, and how lemurs modify their own behaviour based on the social cues they observe. For comparison with simian primate species I will also include a brief note on the performance of these species on similar tasks.

For ease of discussion, specific experiments will be referred to by the chapter in which they appeared and the order in which they were described. For example, "experiment 3.2" denotes the second experiment of chapter 3.

6.1.1 – Do lemurs seek information by attending to others?

In what contexts do lemurs visually refer to others?

I presented lemurs with ambiguous and unambiguous foraging contexts in experiment 3.2 by giving them foods with which they were familiar or completely unfamiliar. Subjects did not reliably spend more total time looking at their testing partner when presented with novel, as compared to familiar, foods, but they did use a different looking strategy in these two conditions. When lemurs were given familiar food, they looked to their testing partners in frequent, but short, glances. However, when given foods with which they had no experience, each individual glance to their testing partner lasted longer. It has been argued that longer individual glances serve to allow an observer to extract more information about causal relationships, the

consequences of actions, and other types of information that would be more difficult to gather by using a cursory monitoring strategy (Cohen, 1972; Range & Huber, 2007). As lemurs exhibited longer individual looks when presented with novel food, I suggest that they were able to recognise an unfamiliar situation as such and seek potentially useful behavioural cues from other individuals in a way comparable to what has been described in human developmental literature as 'social referencing' (Feinman, 1982). Marmosets have also been shown to use a monitoring strategy involving long individual glances when watching conspecifics engage in problem solving tasks, but not when watching conspecifics engage in exploratory behaviour (Range & Huber, 2007), indicating that lemurs and monkeys share the capacity to recognise instances in which useful information can be gathered and also to then modify their behaviour in order to do so.

Lemurs also showed differences in their visual attention when presented with ambiguous social situations (experiment 4.1). I established a 'normal' interaction of allowing subjects to consume raisins that I handed to them (baseline condition) and measured their latency to look to my face. When presenting lemurs with an anomalous social interaction (test condition) in which I instead took the raisin away from them, I found that lemurs looked to my face more quickly. This was despite the fact that the lemurs' desired object (the raisin) was not located anywhere near my face. The differential looking exhibited in this experiment corroborates the results of experiment 3.2 to suggest that lemurs seek out social information when confronted with ambiguous situations. Studies with simian primates have yielded similar results as monkeys (Anderson et al., 2007), apes (e.g. Leavens et al., 1996; Russell et al., 1997), and typical human children (e.g. Walden & Baxter, 1989; Phillips et al., 1992)

all refer to the face of a human experimenter when presented with an anomaly and, like as the lemurs did in experiments 4.1 and 4.2, engage in gaze alternation.

To what social cues do lemurs visually attend?

I found that lemurs were able to visually co-orient with a photograph of a conspecific looking in a particular direction, indicating that static visual information is sufficient to elicit a gaze-following response. In other words, subjects did not require other information (e.g., auditory cues) in order to look in the same direction as other individuals (experiments 5.1 and 5.2). This is an ability shared with Old World monkeys (Lorincz et al., 1999; Scerif et al., 2004) and apes (Horton & Caldwell, 2006), which have also been shown to follow the direction of gaze of a photographic model.

I also explored to which specific physical cues lemurs responded when co-orienting with others (experiment 5.1) and found that lemurs were able to correctly prioritise head orientation over body orientation when these cues conflicted. Further, this configuration was neither more nor less effective for gaze following than when these cues were in agreement. This is another measure on which lemurs and simian primates behave similarly, as Old World monkeys have been found to correctly co-orient when head and body direction conflict (Lorincz et al., 1999).

The results summarised in this section provide evidence that lemurs are able to employ appropriate visual attention strategies (e.g., looking time and cue prioritisation) in order to gather social information, and that they are also able to distinguish situations in which social information would be beneficial. Evolutionarily,

these are highly valuable skills. Visually attending to others can allow an observer to learn about food palatability or the location of resources, or help an observer predict another individual's next action. But do lemurs use social information for these purposes after they have gathered it? In other words, do lemurs modify their behaviour based on what they see when attending to others?

6.1.2 – Are lemurs able to use social cues to modify their own behaviour?

Are lemurs able to interpret social information regarding food palatability?

I found that when lemurs witnessed another individual reject a food item, they were more hesitant when trying the food themselves (experiment 3.1). That is, they took significantly longer to reach out and grab the same type of food they had just seen a conspecific spit out. This was not merely a consequence of being in the presence of a group member that was not eating. Subjects were quick to try these same foods when a non-eating conspecific was present and they had not previously witnessed that individual reject the food. Despite their sensitivity to group members' disgust reactions, however, lemurs still brought food items to their faces for closer inspection (including sniffing and licking), though the amount of such behaviour could not be measured. In other words, the behaviour of their group members was not enough to elicit food avoidance, which is similar to findings in spider monkeys (Fairbanks, 1975) and vervet monkeys (Cambefort, 1981), but contradicts work with cotton-top tamarins that showed these individuals were sensitive enough to conspcifics' disgust reactions to avoid a preferred food without personal inspection (Snowdon & Boe, 2003)

Lemurs' hesitancy to try food, but failure to avoid the food all together, shows that lemurs are able to incorporate information about food palatability available from others' reactions, but may rely more fully on personal experience, when making their own foraging decisions. However, as the foods used in experiment 3.1 were familiar foods and were treated with an unpalatable, but nontoxic, substance, the risk of tasting these foods themselves was very low for lemurs. It is possible that when confronted with a group member rejecting a novel food, a lemur might go on to avoid that same novel food, rather than merely hesitating to handle it.

Can lemurs use others' direction of attention to locate hidden objects?

In experiment 5.2, I asked whether lemurs would modify their behaviour based on the direction of attention of a conspecific. When I presented lemurs with two barriers, behind one of which food was hidden, I found that subjects used the gaze direction of a photographed conspecific model to select the correct location. When lemurs followed the model's gaze, they were more likely to choose the barrier behind which the food was hidden. But when lemurs did not co-orient with the model they were more likely to choose incorrectly. These results indicate that lemurs' gaze following reactions had consequences for their foraging choices, as subjects modified their behaviour according to another individual's direction of attention. This result stands in contrast to many other studies exploring non-human primates' performance on object-choice tasks. Those studies report that subjects are typically unable to use attentional cues to locate hidden resources, even when these same animals exhibit sophisticated gaze-following capabilities. However, gaze following and choice had never before been analysed in tandem in experiments using an object-choice

paradigm, and the results I obtained by performing this type of analysis suggest that perhaps similar patterns would have been found if the same analysis had been conducted.

Do lemurs modify their gesture use according to a recipient's attention?

Lemurs were unable to use social information to modify their use of a trained pointing gesture (4.1 and 4.2). Lemurs were not quicker to point, nor did they point more frequently, nor did their points last longer when I could see them than when I could not. This was evidently not due to a lack of information about my attentional state because lemurs looked at my face frequently throughout each trial. Subjects simply failed to use this information when pointing. This could be because I was expecting lemurs to use communicatively a trained action that was possibly arbitrary to them. Another explanation for these results, though, is that I was asking them to recognise various attentional states of a human rather than a conspecific, and to modify their behaviour accordingly. As lemurs have been reported not to follow a human experimenter's direction of attention (Itakura, 1996; Anderson & Mitchell, 1999), perhaps my finding that they do not respond to differences in an experimenter's attentional state should not be seen as surprising. Simian primates that have been shown to be capable of visually co-orienting with human experimenters have also been shown to gesture discriminatively based on an experimenter's attentional state (Call & Tomasello, 1994; Kaminski et al., 2004).

I also found that lemurs did not modify their use of gaze alternation, a natural and untrained behaviour, according to my attentional state. One possible explanation is that subjects could have been waiting to engage in attentional contact, which would

require my attention to be directed at them. As such, subjects could have been continually monitoring my attentional state throughout the trial, no matter its direction. Alternatively, lemurs could have been searching for a behavioural cue that would indicate my intention, such as a threatening expression or eating the food myself. In either case, lemurs' use of gaze alternation might not differ depending on whether or not I could see them. Therefore, it remains unclear what information the lemurs were extracting from paying attention to me.

These results show that lemurs are able to follow the gaze of a conspecific in order to locate hidden food items, and that they are also able to use conspecific social cues to help determine the palatability of food before tasting it themselves. Although results regarding lemurs' ability to modify their use of a trained pointing gesture according to a human's attentional state are negative, this topic has not been exhausted and deserves further exploration.

6.1.3 – What do we now know about lemur social cognition?

Although lemurs have often been considered the not-so-intelligent relative of simian primates (e.g., Jolly, 1966), my experiments provide further evidence that this is not the case. For the first time, lemurs have shown an ability to seek out social information in appropriate contexts and also to go on to use that information to modify their own behaviour, both of which are skills associated with social referencing. These results begin to provide much-needed insight into the evolution of the primate mind by filling a gap in the literature that has been left open for many decades.

6.2 – Are lemurs capable of mental state attribution?

When considering the results of research that has focused on a certain animal's socio-cognitive abilities, an audience might wonder whether these findings suggest that this particular species has a theory of mind. 'Theory of mind' is a term that was coined three decades ago by Premack and Woodruff (1978) and is defined as the ability to attribute mental states, such as beliefs, desires, and intentions, to others and to oneself. While the focus of my research was not whether lemurs have a theory of mind, and a satisfying response is outside the scope of a PhD dissertation consisting of six experiments, I will briefly address this issue.

My research explored whether lemurs use visual attention of others to modify their own behaviour. The understanding of visual attention is believed to be an important component of theory of mind, without which it might be impossible to understand mental states such as intentions, knowledge, and beliefs in others (Baron-Cohen, 1991; Kummer et al., 1996). One of the most debated questions, then, is whether non-human primates are able to interpret another individual's direction of attention as an overt behaviour resulting from the internal and, thereby, invisible mental state of seeing (e.g. Povinelli et al., 2003).

It has been argued that it is possible to understand another individual's visual perspective without understanding his "mental perspective" (Byrne & Whiten, 1992), and my data cannot provide evidence that anything aside from visual perspective taking is the case for lemurs. It is possible lemurs can appreciate the relationship between head orientation and the location of some visual stimulus without

understanding the attentional experience of another individual (Horton & Caldwell, 2006). Another individual's direction of attention, and the relationship it has to objects or events in the environment, can be used to give a "primitive" psychology – to make sense of past actions and predict future actions, without needing to understand or invoke the mental states of seeing, belief, or knowledge associated with theory of mind (Baron-Cohen, 1994). This is achieved simply by understanding that attention is directed towards targets, that attention is determined by gaze direction, and that individuals usually act upon (or react to) objects to which they are attending (Baron-Cohen, 1994; Gómez, 1996). This "aboutness" of gaze is a way to deal with the causal link of attention to objects without needing to attribute mental states to others (Gómez, 2005b). A mechanism like this one, however, should not be viewed as vastly inferior to a theory of mind system, as both mentalistic and non-mentalistic interpretations of gaze-object relationships allow an individual to appropriately navigate and manage its social environment and require a great deal of cognitive skill.

Responding to a relation between gaze and targets may already, however, be an adaptation to one primitive, but key, feature of mentalism – so-called "intentionality," defined as the property of mental states to be directed at or point to something other than themselves (Dennett & Haugeland, 1987). Adaptations to "see" others' gaze (an overt behaviour) as directed to targets may have been a starting point for more complex adaptations to code intentional relations in terms of covert mental states (Gómez, 2008).

In experiment 5.2, I found that lemurs preferentially acted on targets to which other individuals attended. I proposed a mechanism called "gaze priming" to account for this behaviour: a stimulus in the environment becomes more salient to an observer after another individual directs its attention toward it, and, as a result, the observer

acts differentially in response to that object. As environmental and social context can influence the precise way in which an individual would respond, the observer does not need to reason about the intentions or belief of that other individual in order to respond appropriately. This is a mechanism on which higher-levels of social cognition such a mental state attribution could be built, but these higher-levels are not necessary for that individual's success in coping with social information. This fits nicely with the ideas presented above: although mental state attribution can be a useful skill for leading a life in a social group, it is not the only way in which an individual can effectively discover, learn about, and respond to stimuli in the environment.

Tomasello and colleagues (2003) suggested that theory of mind is not black-or-white, yes-or-no. Instead, it could be viewed as an umbrella term that covers a wide range of socio-cognitive processes. The task becomes, then, to focus on questions that are more specific than "Does animal Y have a theory of mind?" Instead, focus should be placed on the specific ways in which animals deal with the social environment. I set out to explore the visual attention mechanisms lemurs use when presented with various social cues. While my research shows that lemurs are able to recognise and respond to the external behavioural manifestations of mental states, such as direction of attention, these results cannot provide insight into whether lemurs conceptualise those mental states when doing so. As I have argued, systems that do not involve mental state attribution can be highly sophisticated and produce similar (if not the same) results as a theory of mind mechanism.

6.3 – Individual differences

Although individual differences in performance are traditionally ignored in discussions of primate cognition, I feel it is an important topic to discuss here as my dissertation concerns two species that have not been tested in experiments exploring social cognition.

While some individual differences recorded in my dissertation are possibly explained by the sex of the animal (e.g., looking time in experiment 3.2) or the number of trials completed for a specific subject (e.g., looking time in experiment 5.1), there remain a few instances in which some lemurs failed to behave as the rest of the group did for which it is more difficult to account. Sometimes a lemur or two would perform in a way supporting the null hypothesis (e.g., latency to looking to my face in experiment 4.1), while the majority of subjects' behaviour supported a rejection of the null hypothesis. In other experiments the opposite occurred, as it was the majority of subjects that supported the null hypothesis and just one or two others who broke away from this pattern (e.g., gaze alternation differences in experiments 4.1 and 4.2).

Most researchers recognise that some differences in performance are attributed to natural variation (a phenomenon upon which Darwin's theory of evolution depends) and allow for this in their data. Rather than expecting all subjects to behave in exactly the same way, they instead look for patterns within their subject set, sometimes explicitly mentioning they have done so (e.g., "The results indicate that, allowing for individual differences, capuchins are able to…" (Vick & Anderson, 2000)).

In lemurs, experimenters have reported high variability in tactics used to cope with a competitive experimenter. In studies conducted by Genty and colleagues (Genty & Roeder, 2006; Genty et al., 2008), the researchers reported that each subject

developed a different method to deal with a problem of competition with a human. Some lemurs withheld information by not pointing at all, others refused to participate in the study, and others sometimes exhibited deceptive pointing. These differences in strategy could not be explained by the age, sex, or rearing history of the animals.

Differences in individual subjects' performance are also found in ape studies. In their object-choice task, Itakura and colleagues (1999) reported that three out of four chimpanzees improved as the task was modified, while one did not. Zimmerman and collaborators (In press) found individual differences in pointing performance, as two subjects failed to point to a tool that was needed to obtain a food item, while the rest of the group was able to do so. And Tomasello and colleagues (1999) found that while the majority of subjects were able to follow gaze geometrically, there were a few who did not.

These studies provide valuable examples of "a few bad apples" that did not succeed in spoiling the whole bunch, but there are also cases in which the opposite occurred: a minority of subjects that "passed" a task when the rest of the group could not. For example, in their work with domestic pigs, Held and colleagues (2001) found just one out of ten individuals followed a conspecific who had witnessed the hiding of a food item as a strategy to find the food themselves, while the others instead developed a side or positional bias. In this case, the majority of subjects showed no evidence of visual perspective taking, thereby supporting the null hypothesis, while a striking minority of one subject recognised and took advantage of what another individual had seen. This difference was not explained by learning effects or multiple sampling.

Given the high levels of distraction in some environments, due to social pressures for which an experiment cannot control or even the time of year (personally,

I found it nearly impossible to conduct any studies while the lemurs were in breeding season), combined with the natural variation one would expect to find, it is unsurprising to obtain data that varies slightly across subjects. As my dissertation focuses on exploring the competences of lemurs, and not individual lemurs' ability to perform a specific task, this variation does not affect the overall interpretations of my results. It is the fact that the effect was found in most, or even a few, individuals that counts. It shows us that the cognitive capability is there, somewhere, and needs further exploration.

6.4 – But what about the wild?

Another topic worth addressing is how captive experiments relate to how animals in the wild go about their daily lives. In research there is always a trade-off between studying behaviour in a natural setting that does not allow for control of external factors and studying behaviour in captivity under controlled conditions in order to identify the mechanisms involved in cognition (Tomasello & Call, 1997). The conclusions drawn in either case should be slightly cautious as a result.

It has been posited that cognitive demand on an individual varies according to ecological factors, such as food availability and features of the environment (Boesch, 2007). It is possible, then, that the difference in ecological factors faced by wild and captive populations can result in a difference in the manifestations of their true cognitive capacities. For example, chimpanzees may very seldom (if ever) point manually in the wild simply because they have no need to do so (Menzel, 1973). In other words, behavioural cues such as gaze direction, body orientation, and

vocalisations might be enough to solve the problems of every-day life in the wild: locating and acquiring food resources, avoiding predators, etc. For apes in captivity, the story is different. These animals experience limitations to what areas they can access due to cage mesh, etc., and it is common for them to want to obtain items they are unable to acquire on their own. So, a problem for which pointing is the only solution is something apes might only encounter in captive conditions (Tomasello & Call, 1997).

Alison Jolly (1966) has also argued that the wide array of distractions in the environment hinders the ability of animals to attend to specific objects, agents, or events. As a result, wild animals may not discover opportunities to manipulate or otherwise investigate interesting items, limiting the number of chances field researchers have to study an animal's ability to reason about objects or events in their environment. The controlled conditions associated with captivity, however, make it easier for a subject to notice and take interest in whatever it is a human experimenter wants them to, allowing for more thorough investigation of their cognitive capacities.

It is possible, then, that certain circumstances allow animals to produce behaviours they might not use in other contexts, but the capacity to produce the behaviour at all must be there from the start (Leavens et al., 1996; Boesch, 2007). It is important to keep in mind, then, that wild individuals must possess the capacity for the cognitive abilities captive individuals show in the laboratory, otherwise the captive individuals would not be able to produce such results in the first place (Jolly, 1966; Poss et al., 2006).

6.5 – In closing…

It has long been thought that, although lemurs have "monkey-type societies" (in other words, many species live in social groups that incorporate kin and non-kin, allowing differential social relationships, dominance hierarchies, etc), lemurs have not evolved "monkey-like intelligence" (Jolly, 1966; Byrne & Whiten, 1988). This led some researchers (e.g., Jolly, 1966) to posit that the demands of social complexity created the conditions necessary for the evolution of cognition. That is, group living came before cognition, and not the other way around. As such, while lemurs live in social groups comparable to those of simian primates, it is possible that they had not yet developed the sophisticated cognitive skills found in these species. However, prosimian primates were typically overlooked in studies exploring social cognition, creating a gap in our understanding of the evolution of social cognition and leaving this theory without crucial evidence.

I found that lemurs refer visually to other individuals in cases of ambiguity, and go on to use this information in foraging situations. Further, I found that lemurs are able to co-orient with conspecifics, using the correct cues when doing so, and can go on to use this information to find hidden objects. Converging evidence from separate but related lines of research produce a larger, clearer picture than any one study can in isolation (Tomasello 1995). By exploring several different but related topics, I have been able to provide strong evidence that lemurs have a greater level of social understanding than previously thought, and are capable of social referencing. Given the evidence also available from research with simian primates, I would like to claim that lemurs do, in fact, have "monkey-like intelligence." So, though the

conclusions arrived at by Jolly (1966) might yet be true, lemur species in general can no longer be used as supporting evidence.

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